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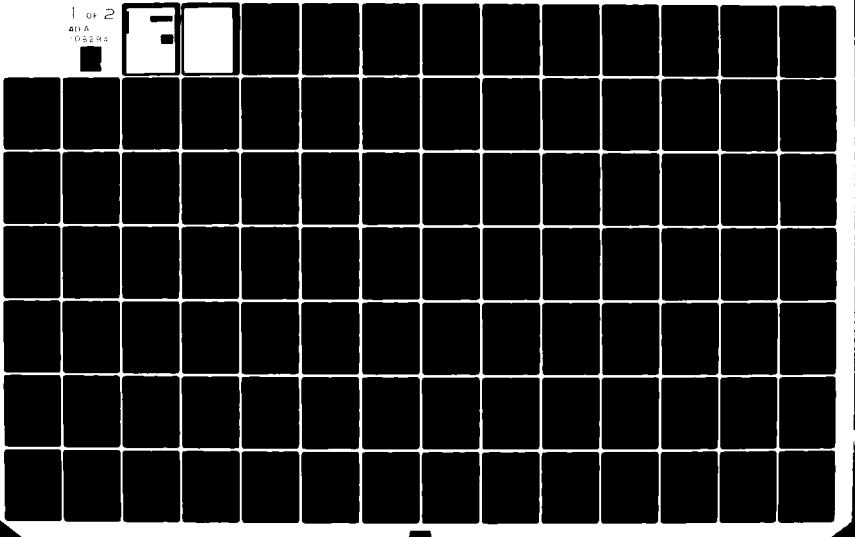

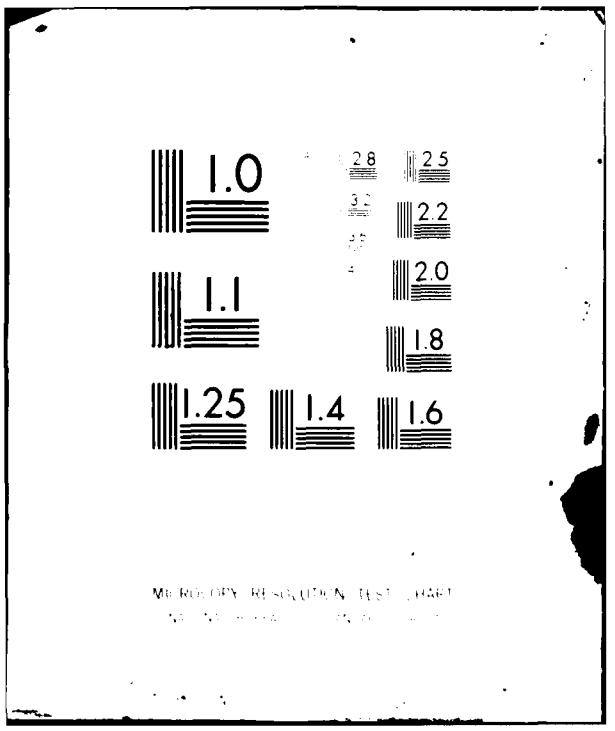
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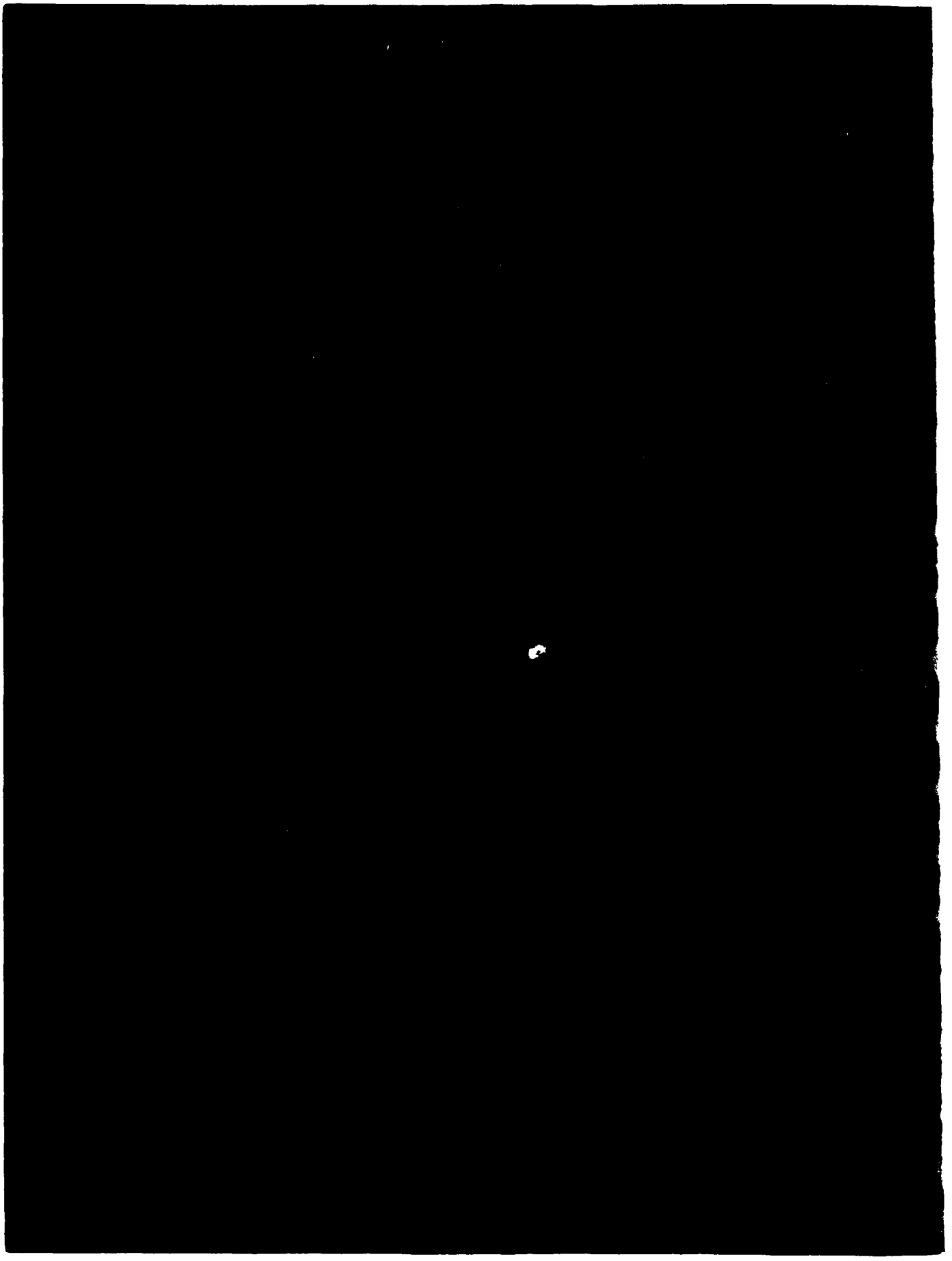

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This document represents a supplement to the Proceedings of the Workshop on Phytoplankton-Environmental Interactions in Reservoirs. The supplement is an attempt to provide a more general perspective and interpretation of present knowledge about phytoplankton behavior in reservoirs and to discuss techniques for reservoir study. A major emphasis of the project was to relate problems and processes to the current state of the art in reservoir modeling. For this reason the last part of Chapter IV is devoted to a

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20. ABSTRACT (Continued).

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The workshop and proceedings were not intended to provide an exhaustive review and in many cases provide citations to other sources of information. Undated references in this volume refer to papers contained in the workshop proceedings.

PREFACE

This document represents a supplement to the Proceedings of the Workshop on Phytoplankton-Environmental Interactions in Reservoirs. The supplement is an attempt to provide a more general perspective and interpretation of present knowledge about phytoplankton behavior in reservoirs and to discuss techniques for reservoir study. A major emphasis of the project was to relate problems and processes to the current state of the art in reservoir modeling. For this reason the last part of Chapter IV is devoted to a summary of formulations used in current models.

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During the conduct of this study and preparation of the report Commanders and Directors of WES were COL J. L. Cannon, CE, and COL N. P. Conover, CE. Technical Director was Mr. F. R. Brown.

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TABLE OF CONTENTS

TABLE OF CONTENTS (continued)

TABLE OF CONTENTS (continued)

LIST OF FIGURES

LIST OF TABLES

I. INTRODUCTION

In October, 1977, the U.S. Army Corps of Engineers initiated the Environmental and Water Quality Operational Studies (EWQOS) program under the sponsorship of the Chief of Engineers and management of the Waterways Experiment Stations (WES). The studies are part of a six-year, $30 million program of applied research designed to address problems associated with the Corps' water resource projects. The fundamental objective of EWQOS is to provide new or improved technology to solve selected environmental quality problems in a manner compatible with authorized project purposes.

As a part of this program the Corps of Engineers contracted with Tetra Tech, Inc. to hold a workshop on phytoplankton behavior in reservoirs. The workshop was held at Asilomar Conference Center, April 10-12, 1979. Fifteen formal papers were given and discussed by participants. Volume I of the project report contains the invited papers. This volume (II) presents a summary, synthesis and analysis of the papers presented and extends some of the discussion to the general open literature.

Although much of the commentary is based on the authors' perception of the workshop consensus, any misconceptions or errors are the responsibility of the authors and in no way are intended to speak for the rest of the attendees.

WORKSHOP OBJECTIVES

The purpose of the workshop was to discuss current concepts and data related to:

1. Understanding the important or key phytoplankton environmental interactions in reservoirs,

2. Determining whether these factors are incorporated in existing phytoplankton algorithms, and

3. Identifying areas requiring additional research.

Thornton* provided a focus for these objectives by describing some potential applications of workshop findings and future goals of the EWQOS program, including:

1. Improve understanding and description of reservoir ecological processes including cause and effect relationships.

2. Develop predictive techniques with estimates of confidence intervals.

3. Demonstrate predictive techniques by application and validation of results.

4. Develop methods to manage various water quality constituents and processes.

If these objectives can be achieved, the methods can be applied in preparing environmental impact assessments, conducting pre-impoundment studies, providing operating criteria for managing reservoirs, and listing data requirements for routine monitoring as well as operation and maintenance.

Inherent in these objectives is the question of whether or not reservoirs are uniquely different from lakes, and further, whether results from lake studies are transferable directly to reservoirs. The consensus of the workshop seemed to be that reservoirs are not uniquely different from lakes in their fundamental processes and that results should be transferable between lake and reservoir studies provided that differences in residence times, hydraulic conditions, sediment loads, etc. are considered. Reservoirs do have one unique aspect that makes them different from lakes and other natural water bodies, and that is the potential for control of inflows, outflows and storage such that

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*Undated references in the text herein refer to papers in Volume I (the Workshop Proceedings). Dated references refer to entries in the references herein, pages 92-98.

water quality might be managed through these variables. Proper design of new reservoirs permits even broader management alternatives. However, any surface water is a unique system with various specific qualities of geology, land form, soil, climate, temperature, morphology, chemistry, and biota that require a site-specific analysis to design realistic management programs.

OVERVIEW OF WORKSHOP PAPERS

The growth and dynamics of a phytoplankton community are controlled by light, temperature, nutrients, species composition of the community, transport phenomena and other biota. The first paper, by Bierman, provided a review of processes and formulations related to nutrient kinetics with emphasis on the comparison between fixed and variable stoichiometry models. The next paper, by Goldman, reviewed current knowledge and practice related to the effects of temperature on phytoplankton dynamics. The third paper, by Lehman, provided a discussion of current and suggested approaches to modeling zooplankton-phytoplankton interactions. The relative importance of mass transport as compared to kinetic factors using both theoretical concepts and field data was discussed by Di Toro. Megard discussed the importance of light and its relation to mixed depth in controlling algal production. A review of current models and approaches to combining the various ecological processes was provided by Park and Collins. A paper by Scavia then provided some important perspectives on the use and interpretation of model results. Particular attention was given to transfer rates between state variables.

The remaining papers provided background on reservoir behavior and use of bioassay techniques. Harris related the importance of physical and nutrient conditions to phytoplankton production in Hamilton Harbour. Nitrogen fixation rates in two southwestern reservoirs were described by Lawley. Kimmel and White provided an initial evaluation of DCMU-enhanced chlorophyll fluorescence as an indicator of phytoplankton physiological status. Poppe et al. provided a brief review of phytoplankton effects on

reservoir use, and Porcella and Cleave provided a review and comment on the use of algal bioassays.

Taylor et al., Lambou et al., and Hern et al. provided a description and analysis of data from the U.S. EPA National Eutrophication Survey related to phytoplankton and temperature, nutrients, and light attenuation. Taken as a whole, the workshop papers provided a perspective on the current "state-of-the-art" in reservoir phytoplankton evaluations.

II. PHYTOPLANKTON EFFECTS ON WATER QUALITY

Phytoplankton have a central role in determining the suitability of reservoir water quality for various project purposes. Phytoplankton influence variables such as dissolved oxygen, transparency, taste and odor, and suspended solids, that can have an effect on many reservoir uses. Reservoir waters used for industrial and domestic water supply and for recreational-aesthetic use can be greatly affected by algal blooms.

Although macrophytes and other primary producers are important in specific reservoirs, in general, phytoplankton form the basis of the food chain and the composition and magnitude of the phytoplankton community have an impact on other biotic groups. Analysis of the role of phytoplankton in controlling and affecting water quality provides an example of the interactive nature of many different variables such as nutrients, light, temperature, mixing regimes, etc. in aquatic ecosystems.

With the proper basis for understanding and simulating phytoplankton behavior in reservoirs, management and control can be improved.

This chapter provides a discussion of some important aspects of phytoplankton-reservoir interactions and effects on water quality.

MIXING, VERTICAL ZONES AND CLARITY

Lakes and reservoirs are not homogeneous systems. Chemical, physical and biological variables vary according to season, time of day, depth, and distance from shore. Littoral areas behave differently from deep waters because of euphotic zone interactions of water and biota with the substrate. Solar energy input causes a gradation in temperature and photosynthesis from the surface water to the bottom.

These observations have led to classification of zones that possess common characteristics within lakes and reservoirs. The euphotic zone includes surface water to a depth where light is reduced to a level that maximum photosynthesis is equivalent to respiration (compensation point). Various compensation points have been used, and the most accepted is relatively arbitrary but simple to determine: 1 percent of the incident surface light values. A Secchi disc is often used to measure light penetration or water clarity because of convenience, but Secchi depth is not simply related to light intensity. For example, light intensities at Secchi depth have been defined variously at 5 percent (Hutchinson 1957), 10 percent (Tyler 1968) and 20 percent (Lorenzen 1978) of the incident surface light value.

The mixed layer is a zone that is essentially homogeneous due to vertical mixing. Because of mixing, each algal cell has approximately equal access to light as it is vertically transported by water movements. Lorenzen and Mitchell (1973) defined the mixed layer as the depth of uniform algal distribution. Similarly, Kimmel and White in their paper defined the mixed layer as the depth of uniform nutrient and chlorophyll distribution in Lake Texoma. An important effect of increasing the depth of the mixed layer is to reduce total integral photosynthesis because algal cells spend more time in low light. The deeper the mixed layer, the less average light received per algal cell. Harris showed how phosphorus could act as the ultimate limiting factor while net growth of phytoplankton could be limited by light as the mixing depth fluctuated with time scales of weeks to months.

Although the photic zone can coincide with the mixed layer, these zones more often attain different depths for both physical and biological reasons. The mixed layer typically extends from the surface to the top of the thermocline or other density separation of water layers. The mixed layer or epilimnion can be less than the photic zone in clear

waters or greater than the photic zone when suspended sediments or algal blooms reduce light penetration.

Megard discussed the absorption of light in surface waters and showed that the Lambert-Bouguer law adequately describes attenuation of light intensity (I) with depth (Z) in surface waters:

$$I_Z = I_o \exp(-\varepsilon Z)$$

The extinction coefficient (ε) varies with extinction due to water, phytoplankton chlorophyll, and sediment. As phytoplankton communities grow, the transparency decreases and light limited algal growth becomes more prevalent. The depth of the mixing zone interacts with transparency to exert a significant effect on growth of phytoplankton.

All of these conditions have pronounced effects on water quality in reservoirs. Different layers of water will have different concentrations of water quality variables, such as phytoplankton and chlorophyll concentrations and dissolved oxygen levels, depending on the relative impacts of light, temperature and nutrients. If all variables other than light are optimal, then phytoplankton growth will be controlled by light intensity, which will largely be controlled by mixing depth and transparency. At steady state, chlorophyll-a (C) is a simple function of mixing depth (Z_L):

$$C = \frac{K_1}{Z_L} - K_2$$

where K_1 is a constant to convert biomass to chlorophyll and incorporates an upper limit of photosynthesis per unit algal biomass and assumed constant rate of removal (loss) of algae; also, K_2 is a constant, the ratio of absorption coefficients for the water and for chlorophyll-a.

Some practical relationships between algal productivity and photic zone (Zp) and mixed layer (Z_L) exist: If $Zp < Z_L$, productivity is less than the maximum potential; if $Zp \geq Z_L$, productivity is equivalent to the maximum potential.

Because reservoirs frequently have turbidity problems owing to the topography, geography, and hydrology of the drainage basins, the phytoplankton will frequently be light limited. Nutrient/chlorophyll relationships will not be applicable as in many lakes because light will limit growth. In the workshop both Harris and Megard discussed the effect of light limitation on the growth of phytoplankton in relation to nutrients and concluded that light limitation prevented nutrients from being limiting. Kimmel and White, using DCMU, indicated in their paper that phytoplankton sampled from the darker regions of the mixed zone were approximately equivalent physiologically to surface algae. In Broken Bow Lake, where the photic zone was deeper than the mixed zone, a metalimnetic maximum was observed for carbon uptake, chlorophyll fluorescence, and microbial activity which coincided with a metalimnetic minimum for dissolved oxygen.

In discussing algal assays, Porcella and Cleave pointed out that assays do not measure light limitation effects. Thus they provide an estimate of the potential algal growth for the given water sample based on nutrient limitation only. For example, Harris stated that during the summer approximately 2 units of chlorophyll-a are obtained for each unit of phosphorus in phosphorus limited lakes. This ratio is analogous to the maximum biomass measured in an algal bioassay.

DISSOLVED OXYGEN (DO)

Dissolved oxygen is a major water quality variable that has considerable ecosystem level application. The growth and maintenance of the aquatic community produce and consume oxygen and the nutrients C, N, P, generally according to the stoichiometric relationships originally formulated by Redfield (taken from Stumm and Morgan 1970):

$$106\ CO_2 + 16\ NO_3^- + H\ PO_4^= + 122\ H_2O + 18H^+ \underset{R}{\overset{P}{\rightleftharpoons}}$$

$$\underbrace{C_{106}\ H_{263}\ O_{110}\ N_{16}\ P_1}_{\text{algal protoplasm}} + 138\ O_2$$

Photosynthesis (P) produces oxygen, and respiration (R) consumes oxygen. In pure water at equilibrium with the air, oxygen dissolves to a concentration that varies only with temperature and pressure. Unproductive environments that have little or no organic matter inputs exhibit DO concentrations at equilibrium with air (saturation level).

As nutrient levels increase, DO begins to fluctuate around the saturation level, as photosynthesis dominates during daylight and respiration in the dark. Excessive organic inputs cause waters to be undersaturated in DO. The production of organic material that results from phytoplankton growth eventually leads to net oxygen consumption as the organic matter decays.

Although workshop papers did not deal with DO or its relation to photosynthesis and respiration in detail, several addressed some of the interactive factors. Park and Collins discussed oxygen evolution as a function of light intensity while Goldman concluded that there was no simple relationship between temperature and photosynthetic or dark respiration rates. The generalized relationship of growth rate for algal populations that approximately double with every 10°C rise in temperature is acceptable although for specific algae grown under defined laboratory or field conditions, this relationship may not hold. Temperature influences carbon uptake per unit of chlorophyll-a only at saturating light intensities. However, chlorophyll content per cell apparently increases or decreases depending on species and whether temperature is decreasing or increasing. Nutrient limitations may confound these relationships.

Transport processes have a marked effect on DO concentrations, although this subject was not within the scope of the workshop.

Hutchinson (1957) discussed "turnover trapping" of DO caused by entrainment of cold, high-DO water during spring overturn. Metalimnetic minima occur when river inflow, BOD and nutrients do not immediately mix with the reservoir water. O'Connor and Dobbins (1958) described a depth term in the reaeration process of the oxygen equilibration model typically applied for analysis of discharge and fate of oxygen demanding wastes. Hypolimnetic oxygen demand caused by organic-rich sediments and the settling of organic particles (algae and detritus) through the hypolimnion may result in anaerobic conditions and affect reservoir water quality by producing sulfides, ammonia, taste and odor compounds, and reduced iron and manganese.

Although these processes were not addressed directly in the Workshop, some of the papers dealt with oxygen. Megard discussed how the amplitude of the DO diel oscillation in Mississippi River navigation impoundments was greatest where algae were most abundant. Scavia modeled DO as part of an overall ecosystem model and then used it as one indicator of how well the model performed. Kimmel and White provided data showing that although the mixing zone extended well below the oxycline, the DO began to decrease at approximately the 1 percent light level in Lake Texoma. In Broken Bow Lake, a metalimnetic minimum for DO was observed; however, it coincided with the 1 percent light level and Kimmel and White stated that this commonly occurs where photic zones are deeper than the mixed zone.

PHYTOPLANKTON EFFECTS ON AESTHETICS

Aesthetics deal with perceived beauty. The aesthetics of natural ecosystems are related to human perceptions of qualities that are modified by culture and experience. It is incorrect to evaluate aesthetics in terms of uses or in economic units. Use variables are relative to technological requirements and/or cost/benefit analysis. A decision to provide water treatment that was based on aesthetics would not necessarily have a direct effect on health or economic well-being.

The variables that have been identified as contributing to the beauty of natural waters can be classified into visual and non-visual sensory perceptions. Visual/aesthetic qualities most often associated with lakes and reservoirs are clarity of water and absence of floating materials. Often the visual composite of the setting and the lake affects the aesthetic value of a scene. Non-visual factors include tastes and odors, the "feel" of the water during contact, and temperature. The Water Quality Criteria of 1972 (NAS-NAE 1973) contains the following recommendations:

> "Surface waters will be aesthetically pleasing if they are virtually free of substances attributable to discharges or waste as follows:
>
> - materials that will settle to form objectionable deposits;
> - floating debris, oil, scum, and other matter;
> - substances producing objectionable color, odor, taste, or turbidity;
> - substances and conditions or combinations thereof in concentrations which produce undesirable aquatic life."

Phytoplankton impact aesthetics extensively because of the colors, turbidity, scums and floating mats that can be formed, taste and odor

compounds that result from excessive productivity, and the feedback from excessive algal biomass or objectionable algal species that affect the food chain directly or by changes in water quality.

Generally, increased nutrients result in increased phytoplankton biomass. Management relationships between total phosphorus as exemplifying the most important nutrient and chlorophyll-a as exemplifying phytoplankton biomass are used to predict the need for controlling nuisance levels of phytoplankton. Most of these nuisance levels are associated with aesthetics (unsightly blooms, color, taste and odor, aquatic community changes) but some problems are use associated (shortened filter runs, toxins, fish production).

Although it has become fashionable to treat the phytoplankton community as an entity by relating chlorophyll-a to other state variables the considerable differences in algal physiology, nutrient requirements, spatial distribution, and problems perceived by the user illustrate that phytoplankton communities vary considerably depending on which species are dominant. Some of the properties typically associated with algal dominants can severely inhibit other uses of the water (Table II-1).

Although most lake management approaches are based simplistically on chlorophyll-a as a function of total P, the more complex models separate phytoplankton models into groups based on nutrient limitations (see papers by Bierman, Di Toro, Park and Collins, and Scavia). These models tend to reflect physiological and ecological differences as well as nutrient limitations.

Diatoms require silicon, and the absence of measurable available silica usually precludes their presence as dominants. In their paper, Taylor et al. showed that a diatom genus, Melosira, was the most common dominant alga in lakes studied by EPA's National Eutrophication Survey (NES). Also, Taylor et al. showed that 8 blue-green, 7 diatom and 5 greens and flagellates were the most common genera in these lakes. These lakes were not a random sample of U.S. lakes but principally represented lakes receiving waste waters.

TABLE II-1. TYPICAL PROBLEMS ASSOCIATED WITH PHYTOPLANKTON BLOOMS

Phytoplankton type	Typical macronutrients that limit growth	Water Quality Effects
Diatoms	N, P, Si	Short filter runs during raw water treatment for municipal uses; occasionally blooms cause floating mats, tastes and odors.
Blue greens	P	Demonstrated toxicity to fish and domestic mammals; tastes and odors common in drinking water and flesh of fish; unsightly, decaying mats of algae and scums; interference with normal food chains and changes in fish community composition.
Greens, flagellates, Others	N, P	Increased turbidity; some association with taste and odor problems; some toxicity associated with flagellates; can increase overall productivity of aquatic community.

Blue-green algae are the major nuisance problem in lakes and reservoirs. As discussed by Poppe et al., many blue-green algal species are associated with production of taste and odor compounds. Also, many blue-green algae are not used appreciably by grazing organisms; buoyancy of cells is controlled by gas vacuoles and this causes floating scums and mats; and some species produce toxins during specific environmental conditions. Lawley provided an example of these problems in his discussion of a bloom in Lake Ray Hubbard, Texas.

For these reasons blue-green algae are considered the most serious problem causing group. As a complement to these problems, some blue-green algae are able to fix nitrogen which gives them a competitive advantage over more beneficial algae in nitrogen limited environments. In reality nitrogen may not limit growth of natural phytoplankton communities in reservoirs because blue-green algae can fix needed nitrogen from the atmosphere. Lawley discussed the role of nitrogen fixers in several southwestern Texas reservoirs.

Most other aesthetic and water quality problems in lakes and reservoirs result from the overproduction of phytoplankton. When more algae are produced than can be consumed by a typical food chain, the excess production is degraded by bacterial activity. This reduces the DO and creates conditions where fish kills occur and the community changes to more tolerant, but generally less desirable, organisms.

Poppe et al. discussed treatment techniques that are applied directly to lakes rather than to the nutrient supply. They concluded that reservoir managers are often faced with an immediate problem that requires an immediate solution such as algicides, nutrient precipitation, or variation in reservoir water withdrawal points (downstream versus upstream, epilimnion versus hypolimnion and timing of releases). Effectiveness, costs, and water quality dictate selection of appropriate short-term management processes. However, long-term elimination of nuisance phytoplankton blooms depends on more permanent solutions such as nutrient control.

PHYTOPLANKTON AND OTHER TROPHIC LEVELS

Generally, all ecosystem communities are driven by energy supply (solar transformed to chemical) and require materials for growth (the nutrients, C, N, P, S,.... Si). This view can be summarized by considering that producers transform solar to chemical energy during photosynthesis. Consumers utilize the chemical energy and materials for growth, and decomposers extract chemical energy for growth and recycle materials during decomposition. Phytoplankton represent the major primary producers of most lakes and reservoirs. Lindeman (1942) provided the classical picture of energy transformation in such a food web, showing that the efficiency of the biological energy transformations from each trophic level was generally about 10 percent.

Although consumers can be treated as an entity, it is more valuable when studying aquatic ecosystems to consider a chain of processors such as herbivores, detritivores and predators. As illustrated in Lehman's paper, zooplankton are a sampling-method-defined group and actually represent all of these processes, and the role of each species in the food web should be understood. His paper is a summary of present data and provides needed insight into future experiments and data requirements suitable for developing accurate models of zooplankton-phytoplankton interactions.

Fish are another important group of consumers which are affected by the phytoplankton community. Fish have direct economic significance and their relationships to Corps of Engineers reservoirs have been discussed in detail elsewhere (Leidy and Jenkins 1977). McConnell et al. (1978) present impressive evidence for the relationship between fish yield and primary productivity. They related the net weight gain of rainbow trout, channel catfish, goldfish and tilapia hybrids in small ponds and pools to oxygen produced and showed that net fish production constituted 0.54 to 2.48 percent of gross photosynthesis. However the

trophic relationships between fish and primary productivity have not been developed as clearly as for zooplankton. This may be a result of the difficulties and costs of accurately assessing productivity and a standing crop of fish (Ricker 1975).

Most empirical relationships of fish and phytoplankton production are based on generalized variables that reflect primary productivity. An example is the morphoedaphic index (MEI) which is equal to the ratio of TDS to mean depth ($\bar{z}$) (Ryder 1965). Ryder, et al. (1974) reviewed research that considered TDS to represent the edaphic factors, phosphorus loading, physiography, geology, climate, terrestrial vegetation, aerial fallout of nutrients, and hydrologic patterns. Similarly, the morphometric variable, mean depth, represents light absorption, littoral zone area, geomorphology and its relationships to soil and rock substrata, the mixing (stratification) and photic zones, lake climate and lake dilution capacity.

Oglesby (1977) contended that it would be more logical to assess fish yield in terms of the primary producers. Using literature data and his own data, he showed that a better fit of the morphoedaphic relationships could be obtained by using a chlorophyll variable (Chls = chlorophyll-a + pheophytin) than by using TDS. Chls would be functionally less removed from the actual fish yield or standing crop than would TDS. However, he stated from a management point of view that low TDS, high mean depth and large lake areas were generally associated with low fish yields and the converse were associated with high fish yields. Thus, he applied the MEI concept and predicted fish yield.

Jenkins (1967) used the MEI as a predictor of fish biomass in southern U.S. reservoirs. In later work he and his colleagues subdivided reservoir types according to sulfate/chloride versus carbonate/bicarbonate dominated TDS and applied residence time (storage ratio) measurements to refine predictions (Jenkins 1977). Because reservoirs frequently display unstable fish populations during early years of impoundment, Jenkins (1977) used the MEI to show that the final predicted biomass is asymptotically approached with time.

The relationships defined by Ryder, Oglesby and Jenkins (with some appropriate unit conversions) are summarized in Table II-1. It is clear that nutrients and primary production are important aspects of fish production and the input of nutrients into lakes is correlated with TDS (e.g., Beeton 1965). These edaphic factors cause increased fish production as reflected by increased yield or biomass. The predictive relationships explain a high fraction of the variance (R^2 = 0.59-0.84) in estimating fish communities and, therefore, can be used for cost-effective management purposes. For reservoirs the slope values indicate the large scale effects of various operational and water quality variables on biomass.

Because other variables may limit biomass and because high TDS may eventually limit growth, the ranges of TDS over which Jenkins' equations for reservoirs were derived also are listed in Table II-2.

In using these relationships, it is important not to neglect assessing the biological and ecological relationships of fish. Eggers et al. (1978) show that fish production in Lake Washington is controlled by the specific food chain routes available to the fish species that are present. Prey switching by the fish apparently resulted in only a slight effect on the response of the fish community to trophic changes. The changes in algal production resulting from reduced nutrient input to Lake Washington were not reflected in fish production changes. This lack of change may have resulted because the blue-green algae that occur under eutrophic conditions do not contribute to the consumer levels of the food chain. Apparently, detrimental effects of blue-green algal production occur only under hypereutrophic conditions. Also, fish production is apparently controlled by other variables when primary production itself does not limit secondary production.

In summary, the fishery of a reservoir depends, as do all consumer species, on the production of biomass through photosynthesis. Various management level models exist for predicting fish biomass and yield from

TABLE II-2. SELECTED RELATIONSHIPS BETWEEN FISH AND MORPHOEDAPHIC FUNCTIONS IN LAKES AND RESERVOIRS

Equation* (log = $\log_{10}$)	R^2	Applicable Range of TDS, mg/ℓ	Reference
a) North temperate lakes, n = 24			
$\log Y_1 = \log 0.97 + 0.446 \log X_1$	0.73	not given	Ryder et al. 1974
b) Hydropower mainstream reservoirs, n = 52, $\bar{\theta} < 0.165$			
$Y_2 = -431 + 363 \log X_2$	0.74	20-800	Jenkins 1977
c) Hydropower storage reservoirs, n = 45, $\bar{\theta} > 0.165$			
$Y_2 = -269 + 245 \log X_2$	0.81	15-300	Jenkins 1977
d) Non-hydro, carbonate-bicarbonate, n = 43			
$Y_2 = -237 + 248 \log X_2$	0.43	20-400	Jenkins 1977
e) Non-hydro, sulfate-chloride, n = 26			
$Y_2 = -104 + 107 \log X_2$	0.77	25-1600	Jenkins 1977
f) 46 reservoirs ($X_2 < 600$, $X_3 < 28330$, $X4 > 140$)			
$Y_3 = -0.40 - 0.15 \log X_3 + 0.20 \log X_2 + 0.93 (X_4) - 0.31 (X_5)$	0.69	not given	Jenkins 1977
g) Equator to north-temperate, Area > 10 km^2, n = 19, 15, 15, resp.		< 1000	
$\log Y_4 = -0.92 + 1.17 \log X_6$	0.84		Oglesby 1977
$\log Y_5 = -5.00 + 2.00 \log X_7$	0.74		Oglesby 1977
$\log Y_5 = 1.91 + 1.56 \log X_8$	0.59		Oglesby 1977

*$\bar{\theta}$ = residence time, years

Y_1 = fish yield, kg / ha·yr

Y_2 = standing crop, kg/ha

Y_3 = sport fish harvest, kg/ha·yr

Y_4 = fish yield, dry wt, kg/ha·yr

Y_5 = fish yield, kgC/ha·yr

X_1 = TDS, mg/ℓ/$\bar{z}$, meters

X_2 = TDS, mg/ℓ

X_3 = surface area, hectares

X_4 = growing season, days

X_5 = reservoir age, years

X_6 = Chls, mg/m^3

X_7 = primary prod., gC/m^2 yr

X_8 = TDS, mg/ℓ/$\bar{z}$, meters

simple variables if the major state variables affecting fish communities are considered. The morphoedaphic index (MEI) is a useful tool for initiating these evaluations, but should be used with care because fundamentally the fish community is controlled not by an index number but by a set of variables that include light, nutrients and other chemicals, habitat, temperature, and flow.

III. TECHNIQUES FOR RESERVOIR STUDY

DATA COLLECTION

Sampling and Analysis

Standard limnological texts (Welch 1948, Lind 1974, APHA 1976, Rainwater and Thatcher 1960, Vollenweider 1969) can be used to describe typical methods for sampling and measuring the common water quality variables. Because phytoplankton are affected by all variables that act on reservoirs, it is important to identify only those variables that affect phytoplankton significantly. Based on the papers presented in the workshop, the necessary variables (with spatial and temporal variation where appropriate) would include 1) morphometric data (area, volume, depth, reservoir perimeter); 2) hydrologic data (inflows, outflows, evaporation, precipitation, other significant water balance data, and mixing data); 3) physical measurements (incident light, transparency, and temperature); 4) chemical measurements (alkalinity, pH, particulate and soluble forms of organic and inorganic C, N, P, Si; gases, major ions, metals, toxicants); and 5) biological parameters (chlorophyll, phytoplankton species composition, zooplankton species composition and biomass).

Some physical, chemical and biological variables should be analyzed in the field (incident light, transparency, temperature, DO, CO_2, pH) while others should be analyzed as soon as possible after collection (alkalinity, nutrients, chlorophyll, and living organisms). Some phytoplankton and most zooplankton can be preserved; samples for metals analysis can be acidified but should be filtered in the field; bioassays should be performed immediately upon return to the laboratory.

Rate Measurements

The previously listed variables have formed the standard set of variables typically measured in freshwater systems. Most ecological

models deal with these variables. Recent results indicate that signif-cantly more information can be gained by including other measurements that characterize rates of processes which control the quality of water. These processes are included in models and should be accurately measured to provide better representation of ecosystem behavior.

Reservoirs frequently differ from lakes because of the hydrologic regime. Reservoir flows generally are greater than lake flows, and consequently reservoir hydrologic residence times are shorter. Because inflows are so important, reservoirs have a greater component of allochthonous energy input as detritus from the watershed than do lakes. Measurements of particulate organic matter (particulate COD, VSS, POC) in the inflows are, therefore, extremely important for reservoirs.

Phytoplankton are only one aspect of primary production in aquatic ecosystems (Vollenweider 1969). Benthic algae and macrophytes also constitute an important input of photosynthetic energy, particularly in reservoirs; in reservoirs their production must be measured. Techniques include areal surveys and measurement of species specific changes in biomass during the growing season. Phytoplankton production can be measured by DO or ^{14}C techniques.

Although chlorophyll-a is usually used to estimate phytoplankton biomass, it relates closely to productivity since it varies with the growth rate of the algae. It is important to measure pheophytin concentration by acidification of the chlorophyll extract to avoid erroneous interpretation of results due to the presence of chlorophyll degradation products. Both spectrophotometric and fluorometric techniques for chlorophyll can be used. Although extractive methods are more sensitive than in vivo fluorescence, different extraction techniques (acetone, methanol, etc.) must be carefully evaluated. The DCMU technique, as described in the paper by Kimmel and White, shows promise as a means of better characterizing chlorophyll in natural phytoplankton assemblages.

An important issue in any study of an aquatic community is an assessment of the factors that limit growth. Reservoirs are frequently turbid and light limits photosynthetic activity. Megard, Kimmel and White discussed the effects of light limitation in their papers. Definition of other limiting factors is very important because simple models can be used to estimate growth rates of phytoplankton. Bioassays are useful for determining the limiting nutrients and the presence of toxicants. Appropriate methodologies are described in the paper by Porcella and Cleave.

In aquatic environments that are at least moderately productive, nitrogen is rarely the limiting factor because certain blue-green algae can fix enough nitrogen (N_2) to cause another factor to limit overall growth. In most cases compensatory nitrogen fixation by heterocystous blue-green algae is adequate to account for otherwise deficient nitrogen. The first step in assessing the importance of nitrogen fixation is to determine the ratio of heterocysts per vegetative cell. If the ratio is greater than 0.01, measurements of nitrogenase, the enzyme responsible for nitrogen fixation, are indicated. Nitrogen balances are usually not indicative of nitrogen fixation because of the many offsetting loss and gain processes (assimilation, sedimentation, nitrification, denitrification, ammonification) of in-lake nitrogen metabolism.

Nitrogenase activity is measured most commonly by determining ethylene in a gas chromatograph as a product of acetylene reduction. It is not accurate to estimate the mass of nitrogen fixed directly from this measurement because of varying ratios of nitrogen fixed per unit of acetylene reduced (ethylene produced). Rough estimates can be made but it is usually appropriate to make at least some $^{15}N_2$ uptake measurements using mass spectroscopy.

Other phytoplankton related processes that affect water quality are sedimentation, recycling of nutrients, and the overall sediment interaction with overlying water. Macrophytes and invertebrates depend on sediments, especially in the littoral zone, for substrate or habitat and as a source of nutrients. Sediments often have a high organic content

which consumes oxygen and affects chemical concentrations by altering redox potentials. Methods for studying these processes usually involve enclosures. The SOD (sediment oxygen demand) chambers described by Sonzogni et al. (1977) can be used to estimate benthic oxygen and nutrient dynamics in situ. Mass balance techniques also appear useful for phosphorus, heavy metals and silica. Microecosystem approaches appear valuable for measuring sediment effects on mass balances of oxygen and other gases, nutrients and metals (Medine et al. 1979)

Sedimentation processes are difficult to assess. Sediment traps are used but these require careful attention and frequent measurement. In reservoirs that receive high loads of particulate materials, sediment ranges are used that relate reservoir bottom elevations to bench marks. Mass balance techniques have been used for assessing input-output of nutrient materials (P, N) and could be feasibly applied to particulate materials, especially minerals.

Data Sources

As environmental analysis becomes a larger part of governmental procedures and regulatory requirements, information storage and retrieval systems become more important. Characteristics of dams and reservoirs are usually available from the owners: generally federal, state and local agencies, utilities, private or cooperative organizations. Typical federal agencies include the Corps of Engineers (USAE), the Bureau of Reclamation (USDI), Department of Agriculture, and Tennessee Valley Authority (TVA). State water resources agencies oprerate many reservoirs and usually have a compendium of those that they do not own. Local agencies, private and other reservoirs are usually for special purposes such as water supply, flood control, cooling, or irrigation. Reservoir morphometry can usually be obtained from these agencies.

The USGS is the major source of flow data. Also, the operators or owners usually possess much of the flow data. Irrigation companies

(water master) usually account for flow from reservoirs they operate while utilities record hydroelectric flow releases.

The USGS operates the National Stream Quality Accounting Network (NASQAN) along with their network of stream gaging stations. Water quality data are also available from the USEPA through STORET. Stations or regions are defined by coordinates (latitude, longitude) and data are requested from USEPA regional offices.

An important aspect of any reservoir assessment program is an evaluation of the public's view of water quality. Taste and odor complaints, aesthetic problems, water uses and associated water quality problems are all important considerations that must be evaluated although frequently in a nonquantitative way. Local citizen groups (Chamber of Commerce, environmentalist groups, service clubs) and newspapers often provide qualitative information on water quality problems. Secchi disc and fish yield (creel census data) are valuable for developing measurable limnological relationships with public perception.

The means of presenting data for later interpretation depends on the objectives of the study. Usually, data are presented as tables and figures that are organized according to time of collection and location vertically and horizontally. Then the data are compared using averages, t-tests for small numbers of samples, analysis of variance techniques, or other non-parametric tests. Samples collected to meet a specific statistical design provide more information than samples collected in the absence of experimental design. Time and location trends are used to interpret the data. Also, data can be analyzed with computer models that mathematically calculate concentrations of state variables according to the conceptual understanding of the system. This is frequently the best method of interpreting large amounts of data for many variables. Such eventualities as using a computer ecosystem model should be considered in performing the experimental design.

Because of the importance of presenting data for a large number of variables in summary manner, multivariate techniques have been developed that may be very useful to managers in making management decisions. The next section presents a summary of these approaches.

MULTIVARIATE NUMERICAL ANALYSIS

Numerous studies on the occurrence and spatial distribution of phytoplankton taxa, both within and among lakes, have been conducted in an attempt to increase the understanding of the effect of environmental factors on phytoplankton community characteristics.

Multivariate methods can be used, for example, to provide an objective analysis of the response of phytoplankton species associations to gradients in limnological variables. The results from such analyses could be used not only to provide a better understanding of species interactions but also to demonstrate the importance of environmental factors influencing phytoplankton assemblages.

Methods

The most widely used methods for the reduction of large biological data sets to a more usable form are classification, ordination, and multiple discriminant analysis. While these methods differ in their basic approach, they often complement one another in the identification and intrepretation of trends within collections from multispecies populations.

Classification methods are used to distinguish groups of entities (e.g., sample sites) according to similarity of attributes (e.g., species). This involves the use of any one of a variety of indices to express similarity between entities, between an entity and a group of entities and between groups of entities. Selection of an appropriate index requires knowledge of the nature of the data, and several different

measures may be tried before the most appropriate is identified. Classification begins with the compilation of a matrix of similarity coefficients (index scores) between all possible pairs of entities. The most similar pair of entities are combined and the matrix is regenerated. This process is iterative and concludes with all entities joined into a single group. If the resulting groups of similar entities are plotted against some measure of homogeneity a hierarchical arrangement of groups or a dendrogram is provided (Figure III-1). The structure of the dendrogram reflects the trends in species distribution.

Classification methods have been successfully used to identify clusters of species assemblages (sites) which occur within environmentally heterogeneous areas. Reviews of important classification strategies have been presented by Clifford and Stephenson (1975), Williams (1971), Sneath and Sokal (1973), and Goodall (1973), and examples of ecological applications can be found in Hughes and Thomas (1971), Boesch (1973) and Crossman et al. (1974).

Ordination refers to the technique by which entities (e.g., sample locations or collections) are ordered along continua for the purpose of displaying biotic relationships among entities. Initially in this procedure each entity is represented by a point in an n-dimensional space, where each entity is characterized by n attributes, and the distances between entities are consistent with calculated entity scores which reflect comparison of attributes measured at each entity. These points are subsequently projected onto a system of fewer dimensions in a manner such that the entity scores on the new axes (usually two principal axes) reflect the inter-entity distances in the original system of axes and, therefore, the maximum amount of biotic variation is maintained in the projection.

The intended result of these manipulations is that the new axes describe patterns in the distribution of species (attributes) determined

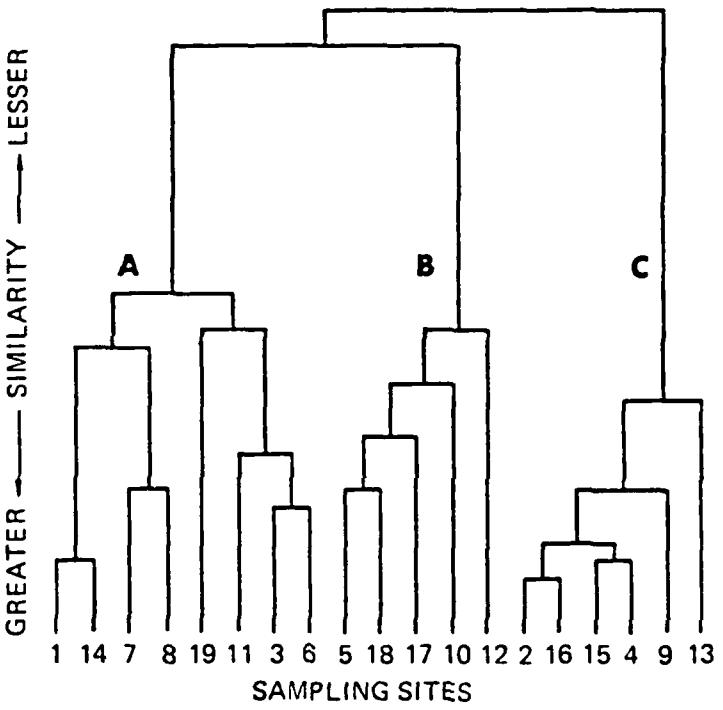

Figure III-1. Cluster analysis of hypothetical survey data set. Three main groups of sampling sites have been defined on the basis of affinities described by similarities in species composition.

by dominant environmental factors. The correlation between these environmental variables and entity scores can be examined using rank correlations or multiple linear regression techniques (Smith and Green 1976). By observing the correlations between the measured abiotic variables and the scores along the axes, associations between environmental parameters and trends in species distribution are evaluated.

The basis of ordination techniques as well as examples of practical environmental applications are discussed by Orloci (1975), Sprules (1977), Smith and Greene (1976).

Multiple discriminate analysis is a method of describing differences between relatively homogeneous species-assemblages and defining the variables which separate these groups. The use of discriminant analysis is described and its advantages are discussed by Pimentel and Frey (1978) and Green and Vascotto (1978).

These methods differ from ordination techniques in that discriminant analysis attempts to define new variables which separate previously defined groups (site clusters). The first step in this process, therefore, involves classification analysis, i.e., the reduction of species-abundance data collected at each site according to biological criteria in order to reflect group affinities. Next individual sites are defined within a K-dimensional space where K represents the number of environmental variables measured at the site. A new variable which is a better discriminant of the groups than the K environmental variables considered singly is then defined. The position of this variable within the multidimensional space is described by a linear function referred to on the discriminant axis. Multivariate analysis of variance and covariance techniques can then be applied to test which environmental parameters provide significant separation of the groups (Green and Vascotto 1978).

Example Application

Examples of analyses of hypothetical survey data using classification ordination and discriminant analysis techniques are discussed herein. The

purpose of these examples is to show the complementary nature of these multivariate numerical techniques and demonstrate their ability to depict relationships between entities or groups of entities and important environmental variables. The survey data in each example include phytoplankton samples collected at numerous lakes in which all species were enumerated. The entities in these examples are, therefore, the sampling sites, while the species counts represent the attributes. At each sampling site a number of limnological variables were measured.

A hierarchical arrangement of groups of sites resulting from an agglomerative-type classification analysis was presented in Figure III-1. The hierarchy in this example is split into three main groups (A, B and C) containing five to eight sampling sites, each with certain affinities defined by similarities in species composition. Following the identification of these groups on the basis of biotic descriptors, further differences among groups could be defined using analysis of variance or multiple analysis of variance techniques to test for differences in mean values of an environmental variable or variables at each site. Alternatively, multiple discriminate analysis or ordination techniques could be applied.

Ordination results for this same hypothetical data set using principal component analysis (PCA) techniques are shown in Figure III-2; the site scores on the first two principal component axes or eigenvectors are plotted. The component which accounts for the greatest amount of variance in the data is designated the first principal component (PCI). Successive components, only one of which is shown (PCII), account for progressively smaller portions of the total variation.

In this example these components summarize the variation in the abundance of species identified at each site. The correlation of individual species with each component can also be determined. Therefore, sites having high abundances of species which show a positive correlation

with a given component and low abundances of species showing high negative correlations with the same component will have relatively high component scores. Importantly, these axes are orthogonal; i.e., entity scores in each axis are independent of one another.

For this example correlations between measured limnological characteristics and ordination scores were tested. Significant correlation coefficients were found for the lake surface area and Secchi depth on PCI and total phosphorus concentrations on PCII. These results are indicated in Figure III-2.

The PCA ordination in this example resulted in the identification of similarities in phytoplankton communities among sites and, more importantly, of patterns in the association between these communities and limnological characteristics. However, the results of ordination analyses must be evaluated with some degree of caution. While the position of entities along the principal component axes suggests a linear relationship between species abundances and the environmental gradient, species abundances actually assume unimodal distributions about environmental optima.

The results of multiple discriminant analysis of the same data are not shown. While the results can be displayed in a similar manner as the results of ordination (Figure III-2), the differences in these techniques are not obvious from the examination of such graphic representation. These differences are primarily related to the fact that separation of individual sites or groups of sites using multiple discriminant techniques is made on the basis of environmental variables. Ordering of sites along axes for display is not done on the basis of biotic characterization, as is the case with ordination techniques. Multiple discriminant analysis initially involves the defining of biotic relationships on the basis of classification techniques.

The multivariate techniques described above vary in their analytical approaches, but their use singly or in concert provide several advantages over more traditional methods of analysis. They represent well defined,

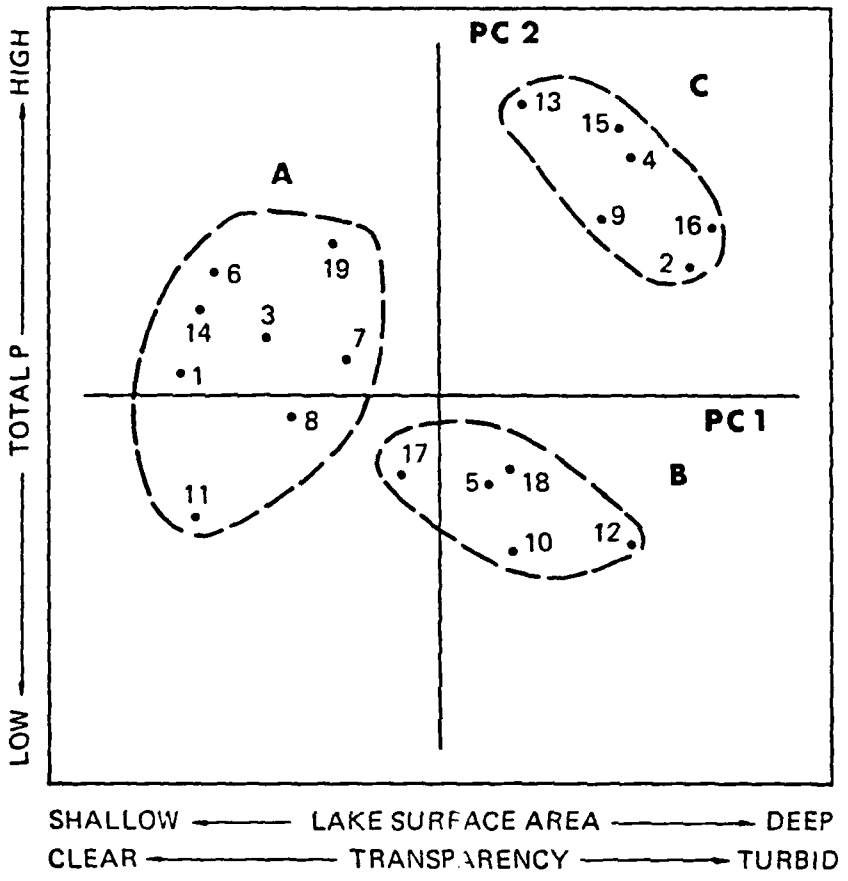

Figure III-2. Results of RCA Ordination. Sampling sites are plotted on principal component axes I and II. Site groups identified in classification analysis are indicated by dashed lines. Lake surface area and Secchi depth were found to be correlated with axis I and total phosphorus concentration was correlated with axis II.

objective methodologies which can be used for efficient reduction of large data bases, concise comparisons of data among sampling stations or surveys, and the description of trends in the relationship between species-associations and environmental variables. The manner in which these analyses lend themselves to visual display is advantageous to the interpretation of data as well as the communication of results to others.

LOADING MODELS

Nutrient loading models combined with chlorophyll and transparency relationships have become a popular approach to lake studies. Although this approach was not included in the workshop it is relevant to reservoir study and is briefly described here.

The major emphasis in recent work has been on phosphorus as often the most important nutrient both because of its effect on algal production and because of its controllability. The basic approach consists of estimating phosphorus loading rates and computing in-lake concentrations with the use of mass balance models and then using relationships between phosphorus and chlorophyll to predict expected chlorophyll levels. Some researchers have carried this further to relate chlorophyll to transparency.

This approach is relatively easy and is a good first step in any lake evaluation. However, a recent Environmental Protection Agency project (Lorenzen 1979) has shown that there are significant difficulties in making generalizations about different lakes. Based on National Eutrophication Survey data it was shown that phosphorus retention coefficients and phosphorus-chlorophyll-a relationships did not conform well to previously suggested relationships. It appears that each lake would require site specific study.

SIMULATION MODELS

Detailed water quality/ecological simulation models offer a considerably more comprehensive and complex tool for evaluation of lake/reservoir systems. The next chapter discusses some of the important aspects of such models.

IV. RESERVOIR PHYTOPLANKTON MODELS

Mathematical models of plankton production have taken several forms and are available in varying degrees of complexity. It is important to understand that different models are appropriate for different uses. The simplest mass balance or nutrient loading models are useful in predicting the long term general effects of changes in nutrient loads but do not address factors such as algal abundance, species composition, succession, intertrophic relationships or effects on dissolved oxygen.

Early models of plankton production concentrated on photosynthesis and rates of primary production. Oceanographic work was particularly useful in pointing out the concept of a "critical" depth (Sverdrup 1953) and the importance of light attenuation and the mixed depth. More recently a number of complex simulation models have been developed. These models contain a variety of state variables and processes linking transport, chemical composition and biological factors.

UTILITY OF SIMULATION MODELS

The utility and usefulness of ecological simulation models have been subjects of great controversy. A great deal of mistrust may have developed as a result of misuse and overconfidence and reliance on model results alone. Model results should be interpreted and evaluated in light of limnological knowledge and the basis and assumptions of the model. When using simulation models it must be kept clearly in mind that the model simulates behavior according to the processes and formulations specified. Frequently, simplifying assumptions are made which will bias results. For example, a vertically mixed assumption implies that results should not conform to prototype behavior in areas where stratification persists. Deterministic models are simply an ordered

set of equations which are based on the knowledge and information available. They represent an attempt to simulate a large number of interactive processes based on knowledge about individual components.

The selection of important processes and conditions to simulate as well as specific formulations depends very much on the questions being asked and the site specific case being studied. One approach would be to develop the most comprehensive, detailed and realistic formulations possible and then find by experiment which parts are not significant. However, limitations in time and budgets normally preclude this type of approach. For example, detailed hydrodynamic and mass transport computations are expensive and time consuming and obviously not necessary for small well-mixed reservoirs. On the other hand, flow fields, location of withdrawals and wind induced circulation may be critical processes in controlling plankton production in some large reservoirs.

Simulation models simply solve sets of differential equations as specified by the user. The adequacy and appropriateness of the equations specified are therefore the key issue. Testing and analysis of the implications of various assumptions are therefore an important part of model development and application.

Data Collection Program Design

One of the more important benefits of a modeling approach is that it forces the user to specify input data requirements. For example, many limnologists have conducted extensive in-lake sampling programs without considering rates of input (both hydraulic and constituent mass) or discharge. The model framework clearly shows the need to measure and quantify fluxes across model boundaries.

A modeling framework forces a clear distinction between model boundary condition data (forcing functions), in-lake data for comparison to model output and data needed for specification of process rate coefficients.

The modeling approach also forces cross-discipline considerations. For example, the limnologist may be most interested in the effects of water quality constituents (nutrients, pH, etc.) on the phytoplankton, whereas the engineer may be most interested in dissolved oxygen and only be interested in the phytoplankton because of their effect on oxygen budgets. The ecologist may be interested in phytoplankton species composition from the point of view of trophic relations and food preferences, whereas the engineer may be interested in filter clogging, tastes and odors.

System Understanding

Deterministic ecological models can provide an excellent tool to synthesize and evaluate knowledge of aquatic ecosystems. By formulating a conceptual framework, specifying components and their interactions, and assigning numerical values to coefficients the hypothetical framework can be evaluated. This is not an easy task, however. It consists of much more than simply adjusting coefficients to achieve adequate "calibration".

Models can provide reasonable comparisons to field measurements of state variables and still grossly misrepresent important processes. Rate coefficients are frequently not fundamental constants and their values thus depend on the formulation. A simple example is the algal growth equation which can be written as a temperature adjusted specific growth rate times other terms for nutrient and light limitation. The value of the specific growth rate constant to give the same net growth rate will depend on whether the other terms are multiplicative, geometric means, or the smallest value is used. By testing a variety of formulations and constants a great deal of insight into the implications of the assumptions can be gained.

Projections and Predictions

To a large extent, managers and scientists would like to use simulation models to predict the consequences of certain actions, be they

management strategies, design decisions or simply no action. This is a very sensitive area and likely to cause mistrust when model results are misused. Unfortunately, it is very difficult if not impossible to quantify the reliability of model predictions. Some variables may be predicted very well and others very poorly. State variables may be simulated accurately but for a combination of incorrect reasons. On the other hand, simulation models are a formal representation of our knowledge and should predict consequences to the best of our ability.

Although simulation models have been developed and refined over the past decade it was generally felt that not enough detailed application and testing have been conducted to consider any one model or set of models a totally reliable predictive tool. This conclusion does not detract from their potential use or future refinement. It simply means more research and development are needed.

As Scavia suggested in the workshop, a five step procedure which involves a range of models, other analytical techniques, and judgment may provide the best predictive methodology.

> "The procedure involves use of simple engineering tools, traditional limnological analyses, and detailed, mechanistic models and is as follows: (1) Use simple mass balance models to estimate future nutrient conditions on the basis of proposed alterations to the water body (e.g., load alterations). (2) Estimate important gross parameters, such as N:P:Si ratios, on the basis of changes in nutrient levels and the geochemical settings of the water body. (3) Use total phytoplankton biomass models to estimate dynamics and magnitude of future algal biomass. (4) Use both traditional analysis of field and experimental data and analysis of simulations with a detailed, mechanistic model to determine controls of plankton and nutrient cycle dynamics under present conditions. (5) Combine results from the above analyses with expert limnological judgment to estimate detailed future conditions."

ALGAL PRODUCTION AND LOSS

Phytoplankton population dynamics constitute a critical component of reservoir ecosystems for a number of reasons including:

- Plankton effects on other water quality variables such as:
  - Dissolved oxygen
  - Nutrient levels
  - pH
  - Transparency
- Plankton effects as base of the food web influence higher predators
- Plankton effects on taste and odors
- Plankton effects on treatability (filter clogging)
- Plankton effects on aesthetics and recreational use.

Many models have been developed to simulate phytoplankton dynamics. The basic approach starts with a simple equation for production and loss.

$$\frac{dP}{dt} = (G-D)P$$

where: P = plankton concentration

G = specific growth rate

D = specific loss rate

t = time.

The differences in models begin when the detailed formulations for the growth and loss rates are considered. Growth rates are dependent on light exposure, temperature, nutrient availability and transport processes. Loss rates depend on temperature, grazing pressure, respiration rates,

sinking rates and other transport processes. All of these factors are species specific and are not necessarily independent of each other.

The remainder of this chapter provides a discussion of these various processes and model formulations.

TRANSPORT

Because phytoplankton are transported with water movements the processes associated with physical movement are frequently very important. The importance, however, depends on the physical system under study. In shallow well-mixed ponds, transport is probably minor in affecting net production. In large deep reservoirs, horizontal and vertical transport are both important and are influenced by wind characteristics as well as inflow-withdrawal conditions.

The general three dimensional form of the transport equation is:

$$\frac{\partial P}{\partial t} + \frac{u\partial P}{\partial x} + \frac{v\partial P}{\partial y} + \frac{w\partial P}{\partial z} - \frac{\partial}{\partial x}\left(E_x \frac{\partial P}{\partial x}\right) - \frac{\partial}{\partial y}\left(E_y \frac{\partial P}{\partial y}\right) - \frac{\partial}{\partial z}\left(E_z \frac{\partial P}{\partial z}\right) = (G-D)P \qquad \text{(IV-1)}$$

where: P, G, D, and T are as previously defined, u,v,w are the velocities in the three coordinate directions x,y,z; E_x, E_y, E_z are the dispersion coefficients in the three directions which parameterize the mixing motions not included in the advective field specification.

Plankton settling can be included in the vertical advection term on the left hand side or included as a portion of D, the phytoplankton loss rate.

The relative magnitudes of the various terms in the transport equation are different for different systems. Figure IV-1 illustrates the magnitude of dispersion coefficients. A rough comparison of dispersion and advection can be made by considering that:

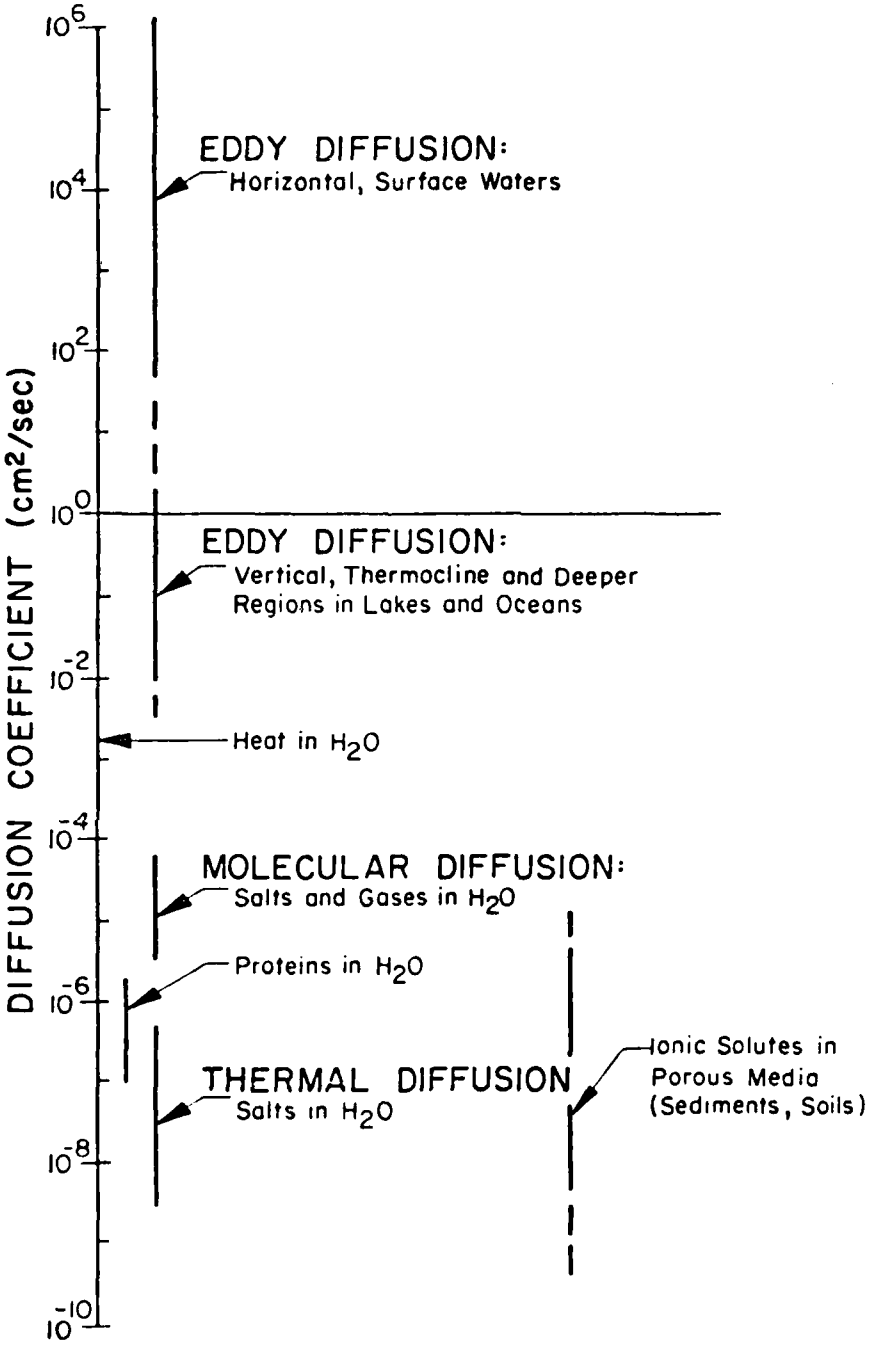

Figure IV-1. Diffusion coefficients characteristic of various environments (redrawn after Lerman 1971).

$$\tau = \frac{X^2}{D} \qquad \text{(IV-2)}$$

where: τ is a mixing time

X = distance

D = Dispersion coefficient

For a one meter distance and a dispersion coefficient of 1 cm^2/sec τ would be

$$\tau = \frac{(100)^2}{1} = 10{,}000 \text{ sec} = 0.11 \text{ day} \qquad \text{(IV-3)}$$

This value for the time to mix one meter can be contrasted to a one meter per day settling velocity.

Vertical dispersion coefficients have been estimated by a number of researchers and include formulations which consider wind speed, density gradients and temperature. Zison et al. (1978) have provided a review of formulations used in estimating dispersion coefficients.

Settling rates of algal cells have emerged as a very significant issue. Di Toro has provided a theoretical analysis of the relative importance of vertical dispersion, growth rates and sinking velocities. None of the presently available models have adequately addressed the issue of sinking velocities. As noted by Park et al., models that consider the environmental control of buoyancy in blue-green algae are presently not available. Sinking velocities are typically set equal to a constant rate which may or may not be temperature dependent. It is interesting that although sedimentation may be an important transport process which regulates net production and species composition, very little research has been conducted in this area (see Park et al. for a brief review).

The selection of appropriate model dimensions and scales is a difficult task. Consideration must be given to spatial variation in the

prototype, the importance of mass transport in affecting that variation, and the availability of appropriate models. A recent review by Orlob (1977) indicates that a well-developed capability exists for simulating two-dimensional circulation and water level fluctuations in shallow, vertically mixed impoundments.

Two-dimensional models in the vertical plane have also been developed (Street et al. 1977). These may be appropriate for long, narrow reservoirs. A number of vertically layered models are also available (see Orlob 1977). However, the more detailed water quality/ecological simulation models have not had extensive application in conjunction with any of the more complex transport models.

TEMPERATURE

The role of temperature in phytoplankton ecology has been reviewed by Eppley (1972) and by Goldman in the workshop. Eppley postulated that "temperature does not seem to be very important in the production of phytoplankton in the sea." He further suggested that phytoplankton growth rates in nature are typically well below maximum potential rates. However, primary productivity does not seem to be greatly affected by wide temperature variations (Eppley 1972), and species common to particular geographical environments and seasons have little difficulty in growing, providing nutrients are available (Smayda 1958). For example, blooms of the common neritic diatom *Skeletonema costatum* are typical in temperate coastal waters during the winter when temperatures are between 0°C-5°C (Curl and McLeod 1961, Smayda 1973a). Similarly, numerous neritic diatoms are common in the northern latitudes, having been classified as cold water species by Hasle (1976). At the other end of the spectrum, many tropical species exist that appear only when water temperatures rise above 25°C (e.g., *Nannochloris* sp.).

In addition to affecting phytoplankton growth rates, temperature appears to have an influence on physiology and cell composition. The workshop paper by Goldman reviews some of the physiological observations and notes that nutrient uptake rates and cell size are increased at low temperatures and may compensate for lower cell division rates.

Temperature effects on photosynthesis and respiration are not well understood. Temperature affects photosynthetic rates at light saturation but light levels and temperature also affect chlorophyll content per cell. Rates of respiration are clearly affected by temperature. It is possible that variations in rates of respiration may be more important in determining net algal production than are gross rates of photosynthesis.

The workshop findings suggested that temperature effects on chemical composition, chlorophyll content, cell size, assimilation numbers, and respiration rates should be better understood in order to address the effects of temperature on phytoplankton growth.

In spite of these complications models of phytoplankton production have been developed and temperature has been included as a rate controlling variable. A number of formulations ranging from linear to exponential have been used. Essentially any curve can be used, and in fact, numerical "look-up" tables may be more efficient in terms of computer time. The problems are still associated with our knowledge of how temperature affects the rates of the various processes rather than how to write equations.

Models must not only consider what effect temperature has on various rate processes but also be able to simulate the temperature regime to which the organism will be exposed. Temperature is frequently computed along with transport calculations and has similar choices associated with determining appropriate scale and dimensions. Because thermal stratification is so important in affecting algal production, reasonably

good temperature predictions can be a critical factor in achieving good model results.

Most simulation models compute water column temperatures based on a heat budget. Orlob (1977) has provided a good review of heat exchange in impoundments. Surface heat exchange is written as the sum of various processes and represented by the general equation:

$$q_n = q_{sn} + q_a + q_{ws} + q_e + q_h \qquad \text{(IV-4)}$$

where: q_n = net heat energy transfer

q_{sn} = net solar radiation

q_a = net atmospheric radiation

q_{ws} = water surface radiation

q_e = evaporative heat flux

q_h = sensible heat flux

Commonly accepted formulations for the terms in the heat budget equation are well documented (Orlob 1977) and not reviewed here. One difficulty is related to how the radiation terms are distributed with depth in the water column. The absorption spectrum for pure water indicates an almost complete absorbtion of all wavelengths greater than 1.2 μ in the first few centimeters. Nearly all radiation outside the visible range (0.36 μ to 0.76 μ) is absorbed within the upper one meter. As a practical matter it is probably sufficient to subtract a fixed fraction of the total incoming radiation as if it were absorbed at the surface and to attenuate the residual according to Beer's Law.

LIGHT

The importance of light as the energy source for photosynthesis cannot be overemphasized. Available light indisputably affects rates

of photosynthesis and algal production. Different algal groups exhibit different responses to varying light intensities and there is some evidence that adaptation of algal cells is a significant factor (Park and Collins).

Formulations used to describe algal growth in response to varying light levels all show a saturation type of curve, some with a decreasing rate at high light levels. Zison et al. (1978) have reviewed a number of these formulations. Again, mathematical equations can be easily written to fit virtually any type of response desired. The difficulty lies in ascribing observed responses to controlling processes. For example, if a decrease in net production rates is observed near the water surface, is it due to light inhibition or some other physical process? It is also difficult to assign constants to various algal groups because the response of an algal cell to light depends to some extent on recent history (adaptation).

Several researchers (Vollenweider 1965, Lorenzen and Mitchell 1973) have shown that exposure to light can be integrated over depth and a 24-hour day to obtain a simplified expression for a "daily rate". For many simulations, a daily rate of production is entirely sufficient. If diel ranges in dissolved oxygen concentrations are desired, such calculations can be superimposed on the daily calculations without having to conduct long-term, hourly time step simulations.

An important aspect of the effects of light on phytoplankton behavior in reservoirs is the proper prediction of light intensity as a function of depth. It has been clearly shown (Lorenzen and Mitchell 1973, Megard, Di Toro) that the depth of mixing and light attenuation can have a profound effect on net algal production.

Available light is attenuated as it passes through the water column by the water itself, by dissolved substances and by particulates

suspended in the water. Particulates are generally divided into organic and inorganic. A typical equation for light attenuation can be written

$$I = I_o \exp [-(\alpha + \beta_i C_i + \ldots \beta_n C_n) Z] \qquad \text{(IV-5)}$$

where I = light intensity at depth, Z

I_o = surface light intensity

α = attenuation coefficient of the water

β_i = attenuation coefficient for constituent, i

C_i = concentration of constituent, i

The relative importance of each term will be site specific. The larger the total attenuation coefficient ($\alpha + \Sigma \beta_i C_i$) the shallower the mixed depth that will control phytoplankton production.

Measurement of light flux is a difficult problem as a result of the varying wavelengths and difference between illumination and light energy. Selection of appropriate units and devices for measuring radiation available for photosynthesis is complex and difficult. Measures of illumination (foot-candle, lux) have been commonly used. The most appropriate measurement is the total quanta within wavelength limits of 350-700 nanometers in watts/cm^2 (Booth 1976). Unfortunately, past research and easily available instrumentation do not conform to this. The following table (from Westlake 1965) provides some conversion factors so that the best use can be made of existing data.

Active Light 390-710 nm

	Joule/m^2/sec	ergs/cm^2/sec	g cal/cm^2/min	lux
Joule/m^2/sec	1	10^3	1.43×10^{-3}	$\sim 2.5 \times 10^2$
watt/m^2	1	10^3	1.43×10^{-3}	2.5×10^2
g cal/cm^2/min (langley/min)	6.98×10^2	6.98×10^5	1	1.8×10^5
lux or meter candle	4×10^3	~ 4.0	5.70×10^{-6}	1
1 lux = 0.0929 foot candles				

NUTRIENTS

The role of nutrients in eutrophication has been the subject of thousands of scientific papers. As a reult of many theoretical and laboratory research programs attempting to evaluate the effects of nutrients on algal production some fairly simplified expressions have been developed. The simplest and most common is the hyperbolic equation based on Monod or Michaelis-Menton enzyme theory.

$$\mu_{sp} = \mu_{max} \frac{S}{K_s + S} \qquad \text{(IV-6)}$$

where: μ_{sp} = specific growth rate

μ_{max} = maximum specific growth rate

S = nutrient concentration

K_s = half saturation constant

S similar expression is used for each nutrient (nitrogen, phosphorus, silicon) and the terms then combined to reduce the growth rate (minimum, multiplicative, geometric mean).

In a discussion by Mar (1976), the very use of the Monod theory is brought into question. Mar cites observed variations in values for the half-saturation constants, suggesting that the variability may be due more to an improper formulation in the Monod theory than to true variability of algal nutrient requirements. If the change in biomasss per unit time is given as:

$$\frac{dB}{dt} = \mu_s \left(\frac{S}{K_s + S} \right) B \qquad \text{(IV-7)}$$

where B = biomass concentration

K_s = Michaelis-Menten half-saturation constant

S = substrate concentration

μ_s = Maximum specific growth rate

Mar points out that under conditions of large S, greater biomass concentrations result in greater productivity predictions. However, where S becomes very small, Equation (IV-7) approaches:

$$\frac{dB}{dt} = \mu_s \left(\frac{S}{K_s} \right) B \qquad \text{(IV-8)}$$

which implies that an increase in biomass will still result in increased productivity. In fact, regardless of how small S becomes, and how clearly limiting the substrate represented actually is in the prototype, if B is very large, the model will predict substantial increases in biomass. Mar points out, further, that the introduction of a decay term into the expression as:

$$\frac{dB}{dt} = \mu_s \left(\frac{S}{K_s + S} \right) B - K_d B \qquad \text{(IV-9)}$$

or

$$\frac{dB}{dt} = \left[\mu_s \left(\frac{S}{K_s + S} \right) - K_d \right] B \qquad \text{(IV-10)}$$

where K_d = decay rate

does not solve the problem since under the condition:

$$1 >> \left(\mu_s \left(\frac{S}{K_s + S} \right) - K_d \right) > 0$$

the same anomalous growth dependence upon biomass is described. That is, for constant and small S, productivity is a function of biomass.

Mar has suggested an alternative expression which does not depend upon Michaelis-Menten half-saturation constants. The expression is of the same form as the Monod formulation:

$$\mu = \mu_s \left(\frac{\alpha S}{B + \alpha S} \right) \qquad \text{(IV-11)}$$

where α = conversion of substrate to biomass.

It should be noted that as S becomes small, and

$$\mu \simeq \mu_s \alpha S/B, \qquad \text{(IV-12)}$$

$$\frac{dB}{dt} \simeq B\mu_s \alpha S/B = \mu_s \alpha S \qquad \text{(IV-13)}$$

Thus for small S, productivity is not materially affected by the value of B.

There are still a number of potential problems with this type of expression. The primary one is that the phenomena of "luxury uptake" and cell storage of nutrient(s) are ignored. Because the processes of nutrient uptake and cell growth are distinct and cell growth is actually

dependent on intracellular nutrient levels a group of "cell quota" type models have been developed. For example the Droop cell quota expression is:

$$\left(\mu_{sp} = \mu_{max} \quad 1 - \frac{K_q}{q}\right) \qquad \text{(IV-14)}$$

where μ_{sp} = specific growth rate

μ_{max} = maximum specific growth rate

K_q = half-saturation constant

q = intracellular nutrient concentration

In order to combine the cell quota model with external nutrient concentrations the so-called "internal pool models" have emerged. Bierman's paper provides a concise review of this approach. Bierman also points out the importance of the formulations for nutrient recycle kinetics. The availability of nutrients for further growth is dependent on the assumed form of nutrients released.

The differences between the different model formulations can be important in affecting which species or algal group will be predicted to dominate or out-compete other groups. A species with a high uptake rate can remove most of the nutrient from the water and use it for continued growth and thus may dominate a species with a high growth rate but lower uptake rate.

GRAZING

The inclusion of planktonic herbivores in phytoplankton simulation models is often necessary to reasonably simulate the dynamics of the phytoplankton. Unfortunately the life cycle and population dynamics of the zooplankton are extremely complex. The processes involved in

zooplankton grazing include ingestion, assimilation, respiration, excretion, egestion and allocation of effort between reproduction and growth. All of these processes are size, age and species specific. The Army Corps of Engineers has sponsored a thorough review of zooplankton ecology as it relates to reservoir dynamics. These processes are, therefore, not reviewed here.

TYPICAL FORMULATIONS

Many researchers have studied individual processes occurring in aquatic ecosystems and developed various mathematical formulations to describe these processes. The great power of simulation models, however, lies in their ability to simultaneously solve the equations and thus simulate the net effect of all of the processes. The complexity and uncertainty associated with the combined processes also creates the greatest criticism because it is easy to lose sight of the assumptions inherent in the model.

There are a number of trade-offs and approaches which can be used in constructing a model and combining formulations for the different processes. One approach is to describe, in as much detail as possible, all the processes. This approach requires specification of a large number of coefficients and makes it difficult to isolate cause and effect relationships.

Another approach is to attempt to determine the most important or controlling processes and model only those. For example, in reservoirs with very high nutrient concentrations it may not be necessary to model the nutrient cycles or their effect on algal growth.

The type of approach which is most appropriate also depends on the goals of the modeling program. If dissolved oxygen, nutrient concentrations, phytoplankton species composition and effect of various fish stocks are important questions then a detailed simulation model would be appropriate. If only limits on chlorophyll-a or phytoplankton biomass are of concern, then a much simpler model could be used.

The workshop paper by Park and Collins provides a review of some of the important processes and representative models currently available. The following discussion provides a review of formulations commonly used in modeling phytoplankton populations.

PHYTOPLANKTON

Beginning with the basic equation for algal production:

$$\frac{dP}{dt} = \left(G_P - D_P \right) P \qquad \text{(IV-16)}$$

where G_P = specific growth rate, day^{-1}

D_P = specific death rate, day^{-1}

P = phytoplankton concentration, mg/ℓ,

the growth and death terms are usually expanded to account for the effects of growth-limiting conditions, respiration, predation, and settling. In order to incorporate the effects of growth limiting conditions, the maximum specific growth rate is modified. Commonly this is done in a fashion analogous to:

$$G_P = MK_P(T) \qquad \text{(IV-17)}$$

where M = Expression for the growth limitation terms for nutrients, light, and temperature.

G_p = specific growth rate, day^{-1}

$K_p(T)$ = temperature-dependent maximum-specific growth rate, day^{-1}

The specific death rate (D_p) may be separated into a respiration term, a predation term, and a settling term:

$$D_p = R_p + S_p + F_p \qquad \text{(IV-18)}$$

where R_p = specific respiration rate, day^{-1}

S_p = specific settling rate, day^{-1}

F_p = specific predation rate, day^{-1}

The production equation becomes:

$$\frac{dP}{dt} = \left(MK_p(T) - R_p - S_p - F_p\right) P \qquad \text{(IV-19)}$$

Phytoplankton Specific Growth Rate (G_p)

There are several factors which can limit or at least mediate the rate of phytoplankton growth. These are:

- Availability of nutrients
- Light levels
- Temperature
- Availability of silica (diatoms)

It is very clear that some factor or factors must provide a limitation on the rate of growth and replication of algal cells. Obviously, in theory, environmental factors may be optimal and may not provide such

limitation. In this case the biochemistry of the organism determines the rate of growth and replication, and the rate is the maximum or saturated growth rate, K_p. In natural systems, however, non-optimal levels of one or more factors or substances required for growth are likely to cause the rate to be less than K_p.

Several approaches are commonly used to describe the specific growth rate G_p (or μ). This rate is known to be a function of temperature, light, and nutrient concentration as discussed above. Numerous investigators (see, for example, Baca and Arnett 1976, U.S. Army Corps of Engineers 1974, Canale et al. 1976, and O'Connor et al. 1975) have used a specific growth rate formulation of the following general form:

$$G_p = K_p(T)\ r\left(I_s, K_e\right) \prod_{i=1}^{n} \left(C_i / \left(K_{m,i} + C_i\right)\right) \qquad \text{(IV-20)}$$

where $K_p(T)$ = saturation growth rate, a function of temperature, day^{-1}

$r(I_s, K_e)$ = light reduction term due to non-optimal incident light, a function of the saturation light intensity, I_s, and the extinction coefficient, K_e, unitless

i = subscript representing each of the n specific nutrients with potential to limit growth (primarily nitrogen and phosphorus, and sometimes carbon and silica)

$K_{m,i}$ = the ith Michaelis-Menten or half-saturation constant, mg/ℓ

C_i = the ith nutrient concentration, mg/ℓ

Tetra Tech (1975, 1976) and the U.S. Army Corps of Engineers (1974) had used the following growth expression:

$$G_p = \left[K_T\ \theta^{(T-20)}\right] \left[\frac{LI}{L_2+LI}\right] \left[\frac{PO_4}{P_2+PO_4}\right] \left[\frac{CO_2}{C_2+CO_2}\right] \left[\frac{N}{N_2+N}\right] \qquad \text{(IV-21)}$$

where K_T = maximum specific growth rate at 20°C, $days^{-1}$

Θ = temperature coefficient, ranging from 1.02-1.06

P_2 = half-saturation constant for algae utilizing phosphorus, mg/ℓ

N_2 = half-saturation constant for algae utilizing nitrogen, mg/ℓ

C_2 = half-saturation constant for algae utilizing carbon, mg/ℓ

L_2 = half-saturation constant for algae utilizing light energy, $kcal/m^2$-sec

PO_4,N,CO_2 = concentrations of phosphorus, nitrogen, and carbon dioxide, respectively, mg/ℓ (or consistent units with P_2, N_2, and C_2)

LI = incident light level in $kcal/m^2$-sec

The variable LI refers to the available light intensity, which varies as a function of both depth and time.

Chen and Orlob (1975) and Chen and Wells (1975) used this same formulation for the specific growth rate in model applications to Lake Washington, San Francisco Bay Estuary, and Boise River, Idaho.

Thomann, Di Toro, and O'Connor (1974) formulated the phytoplankton growth expression in a similar fashion as follows:

$$G_{p_j} = K_T \cdot T \cdot \left(\frac{2.718\ f}{K_e\ H} \left(e^{-\alpha_1} - e^{-\alpha_0} \right) \right) \left(\frac{N}{K_n + N} \right) \left(\frac{D}{K_D + D} \right) \qquad \text{(IV-22)}$$

where G_{p_j} = growth rate averaged over depth

K_T = maximum growth rate, $days^{-1} {}^{\circ}C^{-1}$

T = temperature, °C

f = photoperiod; ranging from 0.3-0.7 (fraction of a day, unitless)

K_e = extinction coefficient; ranging from 0.1-3.0 m^{-1}

H = depth, m

$\alpha_1 = \frac{I_a}{I_s} e^{-K_e H}$

$\alpha_o = \frac{I_a}{I_s}$

I_s = saturation light intensity, foot candles

I_a = incident light, foot candles

N = nitrogen concentration, mg-N/l

D = phosphorus concentration, mg-P/l

K_n, K_D = half-saturation constant for total inorganic nitrogen and total phosphorus, respectively, mg/ℓ

Thomann, Di Toro, and O'Connor (1975) incorporated a nonlinear temperature-maximum growth rate.

$$K_T = K_{T_r} \theta^{(T-T_r)} \qquad \text{(IV-23)}$$

where T = ambient temperature, °C

T_r = reference temperature, °C

K_T = enzyme catalyzed reaction rate at temperature T, day^{-1}

T_{T_r} = enzyme catalyzed reaction rate at the reference temperature, T_r, day^{-1}

θ = characteristic constant

Here, θ was set equal to 1.066 with a reference temperature of 0°C.

Baca and Arnett (1976) have applied an algal growth rate related to the concentration of the principal nutrients, nitrogen and phosphorus, using a modified Michaelis-Menten expression. The nutrient term formulation is given as:

$$\text{MIN}\left[\frac{C_n}{K_n + C_n}, \frac{D_1}{K_p + D_1}\right] \qquad \text{(IV-24)}$$

where C_n = effective nitrogen concentration, mg/ℓ

K_n, K_p = half-saturation constants for nitrogen and phosphorus, mg/ℓ

D_1 = soluble phosphorus concentration, mg/ℓ

MIN = the minimum value function, MIN $(A_1, A_2, \ldots, A_n) = A_i \leq A_1, A_2, \ldots, A_n$ where $i=1,\ldots n$

The effective nitrogen concentration, C_n, is given by:

$$C_n = \begin{cases} pC_1 + (1 - p)C_3, & C_1 \text{ and } C_3 > \varepsilon_n \\ C_1 + C_3, & C_1 \text{ or } C_3 \leq \varepsilon_n \end{cases} \qquad \text{(IV-25)}$$

where p = preference factor

ε_n = critical nitrogen level

C_1, C_3 = ammonia and nitrate concentration, mg-N/l

Baca and Arnett (1976) also included a multiplicative term to account for the effect of toxic substances as follows:

$$G_t = \frac{K_t}{K_t + T_c} \qquad (IV\text{-}26)$$

where G_T = growth limitation term due to toxic substance

T_c = concentration of toxic substance, mg/ℓ

K_t = toxicity constant, mg/ℓ

Baca and Arnett (1976) included this toxicity term in the specific growth expression because they felt that toxic substances generally inhibit growth rates rather than increase respiration (death).

Canale et al. (1976) have also employed this type of specific growth formulation. Canale's formulation includes a maximum growth term which is temperature-dependent, a light reduction factor, and a modified Michaelis-Menten expression for nutrient reduction effects. Their nutrient reduction term is formulated much the same way as Baca and Arnett's (1976) expression and, in addition, includes a multiplicative term for silicate growth limitation.

In addition to these more common approaches, other investigators have suggested quite different formulations for specific algal growth, G_p. Bierman's (1976) complex model of phytoplankton-growth kinetics includes four phytoplankton groups: 1) diatoms, 2) greens, 3) non-nitrogen fixing blue-greens, and 4) nitrogen fixing blue-greens. Table IV-1 is a qualitative listing of the operational differences among the four phytoplankton types, as given by Bierman (1976).

A unique feature of Bierman's model is that cell growth is considered to be a two-step process involving separate nutrient uptake and cell synthesis mechanisms. Motivation for this variable stoichiometry approach is that an increasingly large body of experimental evidence indicates that the mechanisms of nutrient uptake and cell growth are quite distinct

TABLE IV-1. QUALITATIVE DIFFERENCES AMONG PHYTOPLANKTON TYPES MODELED BY BIERMAN (1976)

Characteristic Property	PHYTOPLANKTON TYPE			
	Diatoms	Greens	Blue-Green (N-Fixing)	Blue-Green (Non N-Fixing)
Nutrient Requirements	P, N, Si	P, N	P, N	P
Relative Growth Rates (optimum at 25°C)	High	High	Low	Low
Phosphorus Uptake Affinity	Low	Low	High	High
Sinking Rate	High	High	Low	Low
Grazing Pressure	High	High	None	None

(Bierman 1976). The model includes carrier mediated transport of phosphorus and nitrogen using a reaction-diffusion mechanism and possible intermediate storage in excess of the immediate metabolic needs of the cell. Specific cell growth rates are assumed to be directly dependent on the intracellular levels of these nutrients, in contrast to the classical Michaelis-Menton approach which relates these rates directly to extracellular dissolved phosphorus.

Bierman (1976) simulated the specific growth rate of phytoplankton, G_p, as the minimum value of the following three functions:

$$G_p = \text{MIN} \begin{cases} G_{max} \cdot f(T) \cdot f(I) \cdot \left[1-\exp(-0.693(P/P_o-1))\right] & \text{(IV-27)} \\ G_{max} \cdot f(T) \cdot f(I) \cdot \left[(N-No)/(KNCELL + N-N_o)\right] & \text{(IV-28)} \\ G_{max} \cdot f(T) \cdot f(I) \cdot \left[SCM/(KSCM + SCM)\right] & \text{(IV-29)} \end{cases}$$

where KNCELL = intracellular half-saturation constant for nitrogen-dependent growth, moles - N/l

KSCM = intracellular half-saturation constant for silicon-dependent growth, moles - Si/l

P = moles phosphorus per phytoplankton cell

P_o = minimum stoichiometric level of phosphorus per phytoplankton cell (mol/cell)

N = moles nitrogen per phytoplankton cell

N_o = minimum stoichiometric level of nitrogen per phytoplankton cell (mol/cell)

SCM = silicon concentration in solution (mol/l)

f(T) = $\theta^{(T-20)}$ where θ = 1.07 for diatoms, 1.08 for green algae, and 1.1 for blue-green algae

T = temperature °C, given by

$$T = TMAX \left\{ 0.5\text{-}0.5 \sin \left[\frac{2\Pi \cdot TIME + \phi}{360} \right] \right\},$$

value of sin argument in radians

TMAX = maximal water temperature during summer, °C

TIME = day of year, 30 day months

ϕ = -1890. Value gives sin (arg) = 0 for Nov. 1. Nov. 1 = day 301.

f(I) = $\left[1/(ke \cdot DEPTH) \right] \cdot \left[e^{-\alpha 1} - e^{-\alpha o} \right]$

$\alpha 1$ = $(Ia/Is)\, e^{-(ke \cdot DEPTH)}$, unitless

αo = Ia/Is, unitless

ke = (1.9/secchi depth) + .17 · TCROP ≃ .633 + .17 TCROP, m^{-1}

Ia = 2000 ft-C, surface incident light level

Is = saturation light level, ft-C

DEPTH = water column depth, m

TCROP = total phytoplankton biomass, mg dry wt/l

A major problem in attempting to simulate a complex chemical-biological process is that the models usually contain coefficients for which direct measurements do not exist. It is possible that more than one set of model coefficients could produce an acceptable "fit". In the transition from single-class to multi-class models, this problem becomes particularly acute because it is no longer sufficient to ascertain a range of literature values for a given coefficient. Multi-class models necessitate the definition of class distinctions within this range. Given such circumstances, Bierman (1976) concludes that many of the coefficients in multi-class models simply must be estimated.

The procedure used in Hydrocomp's (Lombardo 1972) model is to treat the algal uptake of each nutrient separately and then determine which uptake rate causes the smallest phytoplankton growth rate during each time period. Hydrocomp's method assumes a nutrient is limiting for each time period but that the identity of the limiting nutrient may change over successive time periods. This concept, also considered by Bierman (1976), has been considered by Orlob (1974) to be a plausible alternative to the single multiplicative Michaelis-Menten formulation, and is presently used by the U.S. Army Corps of Engineers (personal communication).

Hydrocomp's (Lombardo 1972) expression for phosphate uptake is formulated as:

$$G_{pp} = VMAXP \left(\frac{PO_4}{CMMP + PO_4} \right) \left(\frac{NO_3}{CMMN + NO_3} \right) \qquad \text{(IV-30)}$$

where G_{pp} = PO_4 uptake rate, hr^{-1}

VMAXP = maximal PO_4 uptake rate, hr^{-1}; typically 0.3

CMMP = Michaelis constant for phosphorus; typically 0.0303 mg/ℓ

CMMN = Michaelis constant for nitrogen; typically 0.284 mg/ℓ

PO_4 = PO_4 concentration, mg-P/l

NO_3 = NO_3 concentration, mg-N/l

The PO_4 uptake rate, G_{pp}, may presumably be converted to algal biomass production using chemical equivalence information. Hydrocomp (Lombardo 1972) assumes a constant chlorophyll-a to phosphorus ratio of 0.6.

The expression used for nitrogen limited growth is given as:

$$G_{pn} = VMAXN \left(\frac{NO_3}{CMMN + NO_3} \right) \qquad \text{(IV-31)}$$

where G_{pn} = NO_3 uptake rate, hr^{-1}

VMAXN = maximal NO_3 uptake rate, hr^{-1}; typically 0.7/hr

The following expression is proposed for nitrate uptake under light-limited growth conditions (Lombardo 1972):

$$G_{pL} = VMAXL \left(\frac{ZI}{CLT + ZI} \right) \qquad \text{(IV-32)}$$

where G_{pL} = nitrate uptake rate, hr^{-1}

CLT = Michaelis constant; typically 0.033 langleys

ZI = light intensity, langleys/min

VMAXL = maximal NO_3 uptake rate under light-limiting conditions, hr^{-1}; typically 0.3/hr

Two notable differences in the growth expression used by Thomann, Di Toro, and O'Connor (1974) and the one used by Chen and Orlob (1975) are the terms for light effects and temperature effects. Thomann et al. assume a linear relationship between growth rate and temperature while Chen and Orlob apply an exponential temperature correction expression to adjust temperature-dependent rates:

$$G_p(T) = G_{p(20)}\theta^{(T-20)} \qquad \text{(IV-33)}$$

where T = temperature, °C

θ = characteristic temperature correction constant

Baca and Arnett (1976) incorporate a temperature dependent maximum specific growth rate term similar to that of Tetra Tech (1975).

Assuming neither light nor nutrients are in short supply, Lombardo (1972) defines the growth rate to be directly dependent on temperature. The following expression, as suggested by McCombie (Lombardo 1972), is used:

$$G_p = 0.006T - 0.035 \text{ for: } 28 \geq T \geq 6°C \qquad \text{(IV-34)}$$

where G_p = specific growth rate, hr^{-1}

T = water temperature, °C

Lehman et al. (1975) report another approach to temperature correction of G_p. In their model, which is useful for lakes having ice cover in winter, they assume temperature to be constant over a 24 hour period. For each day during ice-free months, temperature is computed as:

$$T = T_{min} + .5\ T_{max}\left[1-\cos\left(2\pi(D-D_m)/(D_e-D_m)\right)\right],\ D_m<D<D_e \qquad \text{(IV-35)}$$

where D = day of the year

D_m = day the ice cover melts

D_e = day ice cover is established

T_{min} = minimum yearly epilimnetic temperature, °C

T_{max} = maximum yearly epilimnetic temperature, °C

Otherwise, $T = T_{min}$. Temperature-dependent relative growth rates (TD) are represented "by skewed normal distributions".

$$TD = \exp\left[-2.3\left[(T-T_{opt})/(T_{u\ell}-T_{opt})\right]^2\right], \quad T>T_{opt} \qquad \text{(IV-36)}$$

or

$$TD = \exp\left[-2.3\left[(T-T_{opt})/(T_{\ell\ell}-T_{opt})\right]^2\right] \quad T\leq T_{opt} \qquad \text{(IV-37)}$$

where exp(x) = the exponential function, e^x

T_{opt} = optimal temperature, °C

$T_{\ell\ell}$ = lower limit of T, °C

$T_{u\ell}$ = upper limit of T, °C

Lehman et al. (1975) suggest that this is an inexact approach to the Arrhenius equation of enzyme activity that Johnson et al. (1954) suggested may represent the exponential growth phase of microorganism populations.

Lassiter (1975) notes that the approach of Equation (IV-33) assumes a monotonically increasing exponential response of the maximal temperature-dependent growth rate to temperature, although this is a reasonable approximation only over a part of the normal temperature range that an algal cell will tolerate. Actually, growth rates have some time-variable optimal temperature remote from which the growth rate drops off very substantially. Lassiter cites a complex set of formulations reported by Bloomfield at al. (1973) to compute k, a general biotic growth rate (1/day):

$$k = \left(\frac{T_\ell - T}{T_\ell - T_m}\right)^X e^{X\left[1 - (T_\ell - T)/(T_\ell - T_m)\right]} \qquad \text{(IV-38)}$$

$$X = \left(W^2\left[1 + (1 + 40/W)^{1/2}\right]^2\right)/400 \qquad \text{(IV-39)}$$

$$W = \left(\ell n\,(Q_{10})\right)\left(T_\ell - T\right) \qquad \text{(IV-40)}$$

$$Q_{10} = \left(K_1/K_2\right)^{\left(10/(T_1 - T_2)\right)} \qquad \text{(IV-41)}$$

where T_ℓ = upper limiting temperature at which the growth rate is zero, °C

T_m = optimum temperature for growth, °C

T = ambient temperature, °C

K_1 = reference rate constant, day^{-1}

T_1 = reference temperature, °C

Q_{10} = ratio of rate constants at two temperatures, T_1 and T_2

T_2 = temperature at which K_2 is to be determined, °C

K_2 = computed rate constant at T_2, day^{-1}

A number of formulations to compute the algal specific growth rate as a function of light have been used. Some of the formulations estimate photosynthetic rate, but this can be related to growth rate.

Baca and Arnett (1976) have used a light reduction term developed by Vollenweider as a direct multiplier of $\hat{\mu}$ (the maximal growth rate) as follows:

$$\frac{AI}{\sqrt{1 + (AI)^2}} \cdot \frac{1}{\sqrt{(1 + (\alpha I)^2)^n}} \qquad \text{(IV-42)}$$

where A = low light constant; typically 0.00054

α = photoinhibition factor, lux^{-1}

I = light intensity, lux

n = 1 (from studies by Battelle)

Di Toro et al. (1971) report that by averaging the expression (over the euphotic depth and over 24 hours):

$$F\,[I(z,t)] = \frac{I(z,t)}{I_s}\, e^{\left[\frac{-I(z,t)}{I_s} + 1\right]} \qquad \text{(IV-43)}$$

the following expression may be obtained:

$$\mu = \hat{\mu}\, \frac{\bar{F}_{max}\, R(t)}{K_r + R(t)} \qquad \text{(IV-44)}$$

where μ = growth rate

I = radiation at depth z at time t

I_s = radiation intensity at which the maximum specific growth rate is achieved (saturation intensity)

z = depth

t = time

$F[I(z,t)]$ = relative photosynthesis

$\bar{F}_{max}$ = maximum fractional reduction in daily specific growth rate over euphotic depth

$R(t)$ = total daily radiation

K_r = total daily radiation at which half of $\bar{F}_{max}$ is attained

The euphotic depth is taken to be the depth to which one percent of the surface radiation penetrates.

Lehman et al. (1975) cite a function for photosynthesis reported by Steele:

$$P(I) = P_{max} \left(I/I_{opt}\right) \exp\left(1-(I/I_{opt})\right) \qquad \text{(IV-45)}$$

where P_{max} = maximal photosynthetic rate, any productivity units

$P(I)$ = the photosynthetic rate at light intensity I, units consistent with P_{max}

I = the ambient light intensity, cal cm^{-2} min^{-1}

I_{opt} = light intensity for saturated photosynthetic rate, cal cm^{-2} min^{-1}

Lehman et al. (1975) further modify the expression to account for end-product inhibition:

$$P(I,C) = \left[\left(C_m - C\right)/\left(C_m - C_o\right)\right] P(I) \qquad \text{(IV-46)}$$

where C_m = cellular maximum carbon store capacity, mol/cell

C = cellular carbon storage inactive organisms, mol/cell

C_o = cellular growth limiting carbon content, mol/cell

Lassiter (1975) cites a model used by Steele:

$$p = a\, p_m\, I\, e^{1-aI} \qquad \text{(IV-47)}$$

where a = a scaling constant

p_m = maximum photosynthetic rate (same variable as P_{max} in Equation (IV-45)), productivity units

I = ambient light level, cal cm^{-2} min^{-1}

p = photosynthetic rate at light level I, productivity units

The derivation of the equation was not described by Steele, but Lassiter points out that the formulation fits several sets of photosynthesis-light curves and suggests a derivation consistent with the following assumptions (quoting Lassiter (1975)):

"1. The rate of change of p with a unit change in I depends both on the value of p and on the deviation of I from the optimum I (I_m);

2. The rate of change of p with a unit change in I is inversely proportional to I, i.e., the photo-inhibition effect."

The formulation is:

$$\frac{dp}{dI} = \frac{k_p\,(1-I/I_m)}{I} \qquad \text{(IV-48)}$$

Integrating Equation (IV-48),

$$p = p_m \left(I/I_m\right)^k e^{k\left(1-(I/I_m)\right)} \qquad \text{(IV-49)}$$

According to Lassiter, Steele had set k = 1 and $1/I_m$ = a to get Equation (IV-47).

Substituting the exponential light attenuation equation,

$$I_z = I_o\, e^{-1.19\eta_T z} \qquad \text{(IV-50)}$$

where I_z = light intensity at depth z, cal cm^{-2} min^{-1}

I_o = incident light (at the surface), cal cm^{-2} min^{-1}

η_T = overall extinction rate per meter of depth, accounting for water, color, turbidity

z = depth, m

into Equation (IV-47), and integrating over depth (z_e) of the euphotic zone,

$$\bar{p} = p_m \frac{\left(_e\left[1-I_o/I_m\, e^{(-1.19\eta_T z_e)}\right]_{-e}\left(1-(I_o/I_m)\right)\right)}{1.19\eta_T z_e} \qquad \text{(IV-51)}$$

where $\bar{p}$ = the average photosynthetic rate over depth.

Substituting for p_m an equation attributed to Bannister (Lassiter 1975),

$$p_m = 12\, \phi_m\, I_m\, h_c\, C_e \qquad \text{(IV-52)}$$

where 12 = the atomic weight of carbon

ϕ = maximum quantum yield

C = chlorophyll-a concentration

h_c = the rate of light absorption by chlorophyll-a

and substituting

b = C/B

where B = biomass

b = conversion constant, chlorophyll per unit biomass

into Equation (IV-52) and dividing through by B, equation (IV-51) becomes:

$$\pi = \frac{12\ \phi_m\ I_m\ h_c\ b \left(e^{\left[-I_o/I_m\ e^{(-1.19\eta_T z_e)} \right]} - e^{(-I_o/I_m)} \right)}{1.19\eta_T z_e} \qquad \text{(IV-53)}$$

where π = the rate of carbon fixation per unit biomass

Then the specific growth rate subject only to light limitation, $\hat{\mu}'$ is given by:

$$\hat{\mu}' = \eta_a\ \pi \qquad \text{(IV-54)}$$

where η_a = the stoichiometric coefficient relating total biomass to carbon (fixation)

Half-Saturation Constant Values

Table IV-2 lists reported values of the half-saturation constants for nitrogen, phosphorus, silicate, carbon, and light. Other data are also presented in the table including saturation growth rates and saturation light intensities. Table IV-3 presents Michaelis-Menten half-saturation constants as reported by Di Toro et al. (1971). Table IV-4 provides values from Lehman et al. (1975). Table IV-5 shows minimum cell nutrient quotas for some marine and freshwater phytoplankton.

Phytoplankton Specific Death Rate, D_p

The algal specific death rate, D_p, represents all losses of phytoplankton biomass. Losses include endogenous respiration, grazing by zooplankton and other herbivores, settling, parasitization, and stress-induced death.

TABLE IV-2. VALUES FOR THE HALF-SATURATION CONSTANT IN MICHAELIS-MENTON GROWTH FORMULATIONS

Phytoplankton Description	Maximum Specific Growth Rate, (Days^{-1})	HALF-SATURATION CONSTANTS					Reference
		Nitrogen (mg/l)	Phosphorus (mg/l)	Silicate (mg/l)	Carbon (mg/l)	Light (Kcal/m^2/sec)	
Total Phytoplankton	0.2-8.0	0.025-0.3	0.006-0.03	-	-	-	Baca and Arnett (1976)
Total Phytoplankton	2.0	0.025	-	-	-	-	O'Connor, et al. (1975)
Total Phytoplankton	2.5	0.025	-	-	-	-	O'Connor, et al. (1975)
Total Phytoplankton	2.0	0.025	0.005	-	-	-	O'Connor, et al. (1975)
Total Phytoplankton	1.3	0.025	0.010	-	-	-	O'Connor, et al. (1975)
Total Phytoplankton	2.1	0.025	0.002	-	-	-	O'Connor, et al. (1975)
Total Phytoplankton	1.0-2.0	0.025	0.006-0.025	-	-	-	Battelle (1974)
Warm Water	2.0	0.07	0.015	-	0.03	0.002	Tetra Tech (1976)
Warm Water	1.-2	0.05-0.3	0.02-0.05	-	0.4-0.6	0.002-0.004	U.S. Army Corps of Engineers (1971)
Cold Water	2.5	0.01	0.02	-	0.04	0.003	Tetra Tech (1976)
Cold Water	1.-3.	0.1-0.4	0.004-0.03	-	0.5-0.8	0.004-0.006	U.S. Army Corps of Engineers (1974)
Diatoms	2.1 (25°C)	-	-	-	-	-	Bierman (1976)
Small Diatoms	2.7	-	-	0.03	-	-	Canale, et al. (1976)
Large Diatoms	2.0	-	-	0.03	-	-	Canale, et al. (1976)
Green	1.9 (25°C)	-	-	-	-	-	Bierman (1976)
Green	1.9	0.015	0.0025	-	-	-	Canale, et al. (1976)
Blue-Green	1.6	0.015	0.0025	-	-	-	Canale, et al. (1976)
Blue-Green (N-Fixing)	0.8 (25°C)	-	-	-	-	-	Bierman (1976)
Blue-Green (Non N-Fixing)	0.8 (25°C)	-	-	-	-	-	Bierman (1976)
Small Cells Favoring Low Nutrients	1.0	0.3	0.03	-	0.5	0.003	Chen and Orlob (1975)
Small Cells Favoring Low Nutrients	1.5	0.3	0.03	-	0.5	0.002	Chen (1970)
Large Cells Favoring High Nutrients	2.0	0.4	0.05	-	0.6	0.006	Chen and Orlob (1975)
Large Cells Favoring High Nutrients	2.0	0.4	0.05	-	0.6	0.004	Chen (1970)
Readily Grazed Fast Settling	1.5	0.02	0.02	-	0.05	0.003	Chen and Wells (1975)
Not Readily Grazed Not Fast Settling	2.0	0.4	0.05	-	0.8	0.006	Chen and Wells (1975)

(continued)

TABLE IV-2 (continued)

Phytoplankton Description	Saturated Light Intensity (Ft-Candles)	Chemical Composition (fraction by weight) C	N	P	Temperature Tolerance Limits (°C)	Location of Study	Reference
Total Phytoplankton	-	-	-	-	-	-	Baca and Arnett (1976)
Total Phytoplankton	300	-	-	-	-	San Joaquin River	O'Connor, et al. (1975)
Total Phytoplankton	300	-	-	-	-	San Joaquin Delta Estuary	O'Connor, et al. (1975)
Total Phytoplankton	300	-	-	-	-	Potomac Estuary	O'Connor, et al. (1975)
Total Phytoplankton	350	-	-	-	-	Lake Erie	O'Connor, et al. (1975)
Total Phytoplankton	350	-	-	-	-	Lake Ontario	O'Connor, et al. (1975)
Total Phytoplankton	-	-	-	-	-	Grays Harbor/Chehalis River, Washington	Battelle (1974)
Warm Water	-	0.4	0.08	0.015	10-30	N. Fork Kings River, Calif.	Tetra Tech (1976)
Warm Water	-	-	-	-	10-30	-	U.S. Army Corps of Engineers (1974)
Cold Water	-	0.4	0.08	0.015	5-25	N. Fork Kings River, Calif.	Tetra Tech (1976)
Cold Water	-	-	-	-	5-25	-	U.S. Army Corps of Engineers (1974)
Diatoms	-	-	-	-	-	Saginaw Bay, Lake Huron	Bierman (1976)
Small Diatoms	-	-	-	-	-	Lake Michigan	Canale, et al. (1976)
Large Diatoms	-	-	-	-	-	Lake Michigan	Canale, et al. (1976)
Green	-	-	-	-	-	Saginaw Bay, Lake Huron	Bierman (1976)
Green	-	-	-	-	-	Lake Michigan	Canale, et al. (1976)
Blue-Green	-	-	-	-	-	Lake Michigan	Canale, et al. (1976)
Blue-Green (N-fixing)	-	-	-	-	-	Saginaw Bay, Lake Huron	Bierman (1976)
Blue-Green (Non N-Fixing)	-	-	-	-	-	Saginaw Bay, Lake Huron	Bierman (1976)
Small Cells Favoring Low Nutrients	-	-	-	-	-	Lake Washington	Chen and Orlob (1975)
Small Cells Favoring Low Nutrients	-	-	-	-	-	San Francisco Bay Estuary	Chen (1970)
Large Cells Favoring High Nutrients	-	-	-	-	-	Lake Washington	Chen and Orlob (1975)
Large Cells Favoring High Nutrients	-	-	-	-	-	San Francisco Bay Estuary	Chen (1970)
Readily Grazed Fast Settling	-	0.5	0.09	0.015	-	Boise River, Idaho	Chen and Wells (1975)
Not Readily Grazed Not Fast Settling	-	0.5	0.09	0.015	-	Boise River, Idaho	Chen and Wells (1975)

TABLE IV-3. MICHAELIS-MENTEN HALF-SATURATION CONSTANTS FOR NITROGEN AND PHOSPHORUS (FROM DI TORO ET AL. 1971)

Organism	Nutrient	Michaelis Constant, µg/Liter as N or P
Chaetoceros gracilis (marine diatom)	PO_4	25
Scenedesmus gracile	Total N	150
	Total P	10
Natural association	PO_4	6[a]
Microcystis aeruginosa (blue-green)	PO_4	10[a]
Phaeodactylum tricornutum	PO_4	10
Oceanic species	NO_3	1.4-7.0
Oceanic species	NH_3	1.4-5.6
Neritic diatoms	NO_3	6.3-28
Neritic diatoms	NH_3	7.0-120
Neritic or littoral	NO_3	8.4-130
Flagellates	NH_3	7.0-77
Natural association	NO_3	2.8
Oligotrophic	NH_3	1.4-8.4
Natural association	NO_3	14
Eutrophic	NH_3	18

[a]Estimated.

TABLE IV-4. HALF-SATURATION CONSTANTS FOR N, P, AND Si UPTAKE (μM) REPORTED FOR MARINE AND FRESHWATER PLANKTON ALGAE (AFTER LEHMAN ET AL., 1975)

[illegible]	NO_3	0.3-1.9	Carpenter and Guillard (1971)	Leptocylindrus danicus	NO_3	1.25	Eppley, Rogers and McCarthy (1969)
		1.8	MacIsaac and Dugdale (1969)		NH_4	0.7	
		0.35	Caperon and Meyer (1972)	Rhizosolenia stolterfothii	NO_3	1.7	
		0.5	Eppley, et al. (1969)		NH_4	0.5	
	NH_4	0.4		Rhizosolenia robusta	NO_3	3.0	
Dunaliella tertiolecta	NO_3	0.21	Caperon and Meyer (1972)		NH_4	7.5	
	NH_4	0.17		Ditylum brightwellii	NO_3	0.6	
	NO_3	1.4	Eppley, et al. (1969)		NH_4	1.1	
	NH_4	0.6		Coscinodiscus lineatus	NO_3	2.6	
Asterionella japonica	NO_3	0.7-1.3	Eppley and Thomas (1969)		NH_4	2.0	
		1.0	Eppley, et al. (1969)	Coscinodiscus wailesii	NO_3	3.6	
	NH_4	1.0			NH_4	4.9	
Hymenomonas lutheri	NO_3	0.42	Caperon and Meyer (1972)	Euglena gracilis	PO_4	16.	Blum (1966)
	NH_4	0.29					
	NO_3	0.6	Eppley, et al. (1969)	Cyclotella nana	PO_4	0.58	Fuhs, et al. (1972)
	NH_4	0.4					
Fragilaria pinnata	NO_3	0.6-1.6	Carpenter and Guillard (1971)	Thalassiosira fluviatilis	PO_4	1.72	
Bellochia sp.	NO_3	0.1-0.9		Chlorella pyrenoidosa	PO_4	4.-5.	Jeanjean (1969)
Cosmarium sp.	NO_3	0.31	Caperon and Meyer (1972)				
Ankistrodesmus braunii	NO_3	2.6	Ketchum (1939)	Nitzschia actinastroides	PO_4	1.0	Muller (1972)
Anabaena cylindrica	NO_3	70.	Hattori (1962)	Scenedesmus sp.	PO_4	0.6	Rhee (1973)
	NO_2	40.		Pediastrum duplex	PO_4	1.1	Lehman unpublished
Chlorella pyrenoidosa	NO_2	25.	Knudsen (1965)	Dinobryon cylindricum	PO_4	0.8	
Chaetoceros gracilis	NO_3	0.2	Eppley, et al. (1969)	D. sociale var. americanum	PO_4	0.5	
	NH_4	0.4		Nitzschia actinastroides	Si	3.5	Muller (1972)
Gymnodinium polyedra	NO_3	9.5		Thalassiosira pseudonana	Si	1.4-2.9	Paasche (1973a)
	NH_4	5.5			Si	1.39	Paasche (1973b)
Gymnodinium splendens	NO_3	3.8		Thalassiosira decipiens	Si	3.37	
	NH_4	1.1					
Coccolithus huxleyi	NO_3	0.1		Skeletonema costatum	Si	0.80	
	NH_4	0.1					
Skeletonema costatum	NO_3	0.45		Lithophora sp.	Si	2.58	
	NH_4	0.8		Ditylum brightwellii	Si	2.96	
Isochrysis galbana	NO_3	0.1					

TABLE IV-5. MINIMUM CELL NUTRIENT QUOTAS (μMOLES CELL^{-1}) OF P, Si, AND N FOR SOME MARINE AND FRESHWATER PHYTOPLANKTON (AFTER LEHMAN ET AL. 1975)

Phosphorus:		
Asterionella formosa	2×10^{-9}	Mackereth (1953)
	$1.5\text{-}3. \times 10^{-9}$	Muller (1972)
Asterionella japonica	1.5×10^{-9}	
Cyclotella nana	0.9×10^{-9}	Fuhs (1969)
Nitzschia actinastreoides	3×10^{-9} (35μ)**	Muller (1972)
	4×10^{-9} (50-55μ)**	
Phaeodactylum tricornutum	2×10^{-9}	
Chlorella pyrenoidosa	3×10^{-9}	
Scenedesmus quadricauda	4.5×10^{-9}	
Scenedesmus sp.	1.7×10^{-9}	Rhee (1973)
Thalassiosira fluviatilis	12.5×10^{-9}	Fuhs, et al. (1972)
A. formosa	3×10^{-8}	Grim (1939)*
Gymnodinium	1.1×10^{-8}	
Dinobryon	0.5×10^{-9}	
Anabaena	2.5×10^{-9}	
Silicon:		
Navicula pelliculosa	0.5×10^{-7}	Busby and Lewin (1967)
Nitzschia alba	3×10^{-7}	Lewin and Chen (1968)
Asterionella formosa	2×10^{-6}	Hughes and Lund (1962)
	1.8×10^{-6}	Grim (1939)*
Fragilaria crotonensis	4×10^{-6}	
Thalassiosira pseudonana	2×10^{-8}	Paasche (1973a)
Nitrogen:		
Isochrysis galbana	3×10^{-8}	Droop (1973)
Asterionella formosa	6×10^{-7}	Grim (1939)*
Gymnodinium	3.9×10^{-7}	
Dinobryon	1.3×10^{-8}	
Anabaena	1×10^{-7}	

*These quantities are not necessarily the minimum.

**Cell length.

The endogenous respiration rate is the time rate of algal biomass conversion back to carbon dioxide per unit weight of organic carbon content (O'Connor et al. 1973). As a process, it can be considered as the inverse of photosynthesis.

Di Toro et al. (1971), O'Connor et al. (1975), Thomann et al. (1975), and the Fisheries Research Board of Canada (Simons 1976) have proposed a general expression describing the phytoplankton death rate of the following type:

$$D_p = K_2 + C_g Z \left(\frac{K_{mp}}{K_{mp} + P} \right) - \frac{W}{H} \qquad \text{(IV-55)}$$

where K_2 = endogenous respiration rate of phytoplankton, a function of temperature, day^{-1}

C_g = grazing rate of herbivorous zooplankton, 1/day-mg zooplankton carbon

Z = zooplankton carbon concentration, mg/ℓ

K_{mp} = Michaelis-Menten half-saturation constant for zooplankton grazing on phytoplankton, mg/ℓ

W = settling velocity, m/day

P = phytoplankton concentration, mg/ℓ

H = depth for settling out, m

The same investigators and others (Thomann et al. 1974, and Lombardo 1973, in modeling studies of the Potomac and San Joaquin Delta Estuaries), represented the temperature corrected endogenous respiration rate, R (in day^{-1}), as a linear function of temperature as follows:

$$R = K_2 T \qquad \text{(IV-56)}$$

where K_2 = endogenous respiration rate, $day^{-1} {}^{\circ}C^{-1}$

T = temperature, °C

In a modeling study for Lake Ontario, Thomann et al. (1975) proposed the following expression for endogenous respiration:

$$R = K_2 \, \theta^{(T-20)} \qquad \text{(IV-57)}$$

where K_2 = endogenous respiration rate, day^{-1}

θ = temperature coefficient; typically 1.08

The filtering rate, C_g, is known to vary as a function of the size of the phytoplankton cell being ingested, the concentration of the phytoplankton, the amount of particulate matter present, and temperature. However, as an approximation, a single constant grazing coefficient, C_g, is commonly used.

Baca and Arnett (1976) used the following representation for the phytoplankton death rate (day^{-1}) in their water quality model:

$$D_p = F_1 + F_2 \qquad \text{(IV-58)}$$

where F_1 = algal respiration rate, day^{-1}

F_2 = algal decomposition rate, day^{-1}; typically 0.003-0.17

Tetra Tech (1975, 1976) and the U.S. Army Corps of Engineers (1974) consider the phytoplankton death rate, D_p, to be a function of endogenous respiration, zooplankton grazing, and sinking losses. Generally, two values of respiration are available in their formulations. When the temperature is below the lower bound of a temperature tolerance limit, the standard respiration rate is used; otherwise the active respiration rate is used. Tetra Tech (1975, 1976) and Chen and Wells (1975) consider the amount of phytoplankton biomass assimilated by the zooplankton to be a function of both the amount of algae grazed and the digestive efficiency of the zooplankton.

A formulation used by Bierman (1976) for the phytoplankton death rate, D_p, also considers losses to be due to respiration (and cell death), grazing, and sinking. His death term is formulated as follows:

$$R = RLYS \cdot T \cdot TCROP \qquad \text{(IV-59)}$$

where R = rate of phytoplankton biomass loss, day^{-1}

RLYS = algal death rate $(day\text{-}°C\text{-}mg/\ell)^{-1}$

T = temperature, °C

TCROP = total phytoplankton biomass, mg/ℓ

Lombardo (1972) reports an expression for the phytoplankton death rate which is essentially the same as that given by Thomann, O'Connor and Di Toro. Lehman et al. (1975) consider the algal specific death rate to be due to respiration and physiological mortality. The formulation for net algal production is

$$\frac{dN}{dt} = \left[.693\ \mu - (V/D) - M \right] N \qquad \text{(IV-60)}$$

and

$$M = M_{max} \left[1 - \exp(k \cdot SG) \right] \qquad \text{(IV-61)}$$

where N = algal cell concentration, numbers/mℓ

μ = cell division rate, day^{-1}

V = sinking rate, m/day

D = mean epilimnetic depth, m

M = fraction of population dying per day

M_{max} = maximal fraction dying per day at suboptimal condition

SG = number of suboptimal days

k = .693/d

d = number of suboptimal days required for $M = M_{max}/2$

Lassiter (1975) uses the formulation:

$$D_T = \begin{cases} -a \ln k/k_m & , T \geq T_m \\ 0 & T < T_m \end{cases} \qquad (IV\text{-}62)$$

where D = the specific death rate due to excessive temperature, day^{-1}

T = ambient temperature, °C

T_m = optimal temperature, °C

a = scaling coefficient, day^{-1}

and

$$k = \begin{cases} k_m \left[e^{a(T-T_m)}\right] \left(\frac{T_\ell - T}{T_\ell - T_m}\right)^{a(T_\ell - T_m)} & , T \leq T_\ell \\ 0 & , T > T_\ell \end{cases}$$

where k_m = maximal growth rate, day^{-1}

Table IV-6 provides rate values for algal respiration, zooplankton filtering, and algal sinking, and values of the grazing constant and zooplankton digestive efficiency. Values given are for 20°C unless noted otherwise. Tables IV-7 and IV-8 are from Di Toro et al. (1971) and show rates of phytoplankton endogenous respiration and zooplankton grazing rates.

TABLE IV-6. VALUES FOR COEFFICIENTS IN PHYTOPLANKTON SPECIFIC DEATH RATE EXPRESSIONS

Phytoplankton Description	Algal Respiration Rate @20°C (day^{-1})	Zooplankton Filtering Rate @20°C (l/mg-C-day)	Zooplankton Digestive Efficiency (mg/mg)	Sinking Rate (m/day)	Michaelis Grazing Constant (µg chlor/l)	Location of Study	Reference
Phytoplankton	0.035-0.12	-	-	-	-	-	Baca and Arnett (1976)
Phytoplankton	-	-	0.5-0.8	0.-2.	-	Lake Washington	Chen and Orlob (1975)
Phytoplankton	0.08	-	-	0.00-0.005	-	Lake Michigan	Canale, et al. (1976)
Phytoplankton	0.10	0.13	0.6	-	50	San Joaquin River	O'Connor, et al. (1975)
Phytoplankton	0.08	0.25	0.65	-	50	Lake Erie	O'Connor, et al. (1975)
Phytoplankton	0.10	1.2	0.60	0.1	10	Lake Ontario	O'Connor, et al. (1975)
Phytoplankton	0.10	0.18	0.60	-	50	San Joaquin Delta Estuary	O'Connor, et al. (1975)
Phytoplankton	0.10	-	-	-	-	Potomac Estuary	O'Connor, et al. (1975)
Phytoplankton	0.10	-	-	0.4	-	-	Lombardo (1972)
Phytoplankton	0.10:0.02	0.13	-	-	-	-	Di Toro, et al. (1971)
Phytoplankton	0.1	-	-	0.5	-	Boise River, Idaho	Chen and Wells (1975)
Phytoplankton	-	-	-	0.5	-	San Francisco Bay Estuary	Chen (1970)
warm water	0.1 0.01 (active)(inactive)	-	0.7	0.2	-	N. Fork Kings River, California	Tetra Tech (1976)
warm water	0.05	-	-	0.2	-	Lake Washington	Chen and Orlob (1975)
cold water	0.1 0.01 (active)(inactive)	-	0.7	0.05	-	N. Fork Kings River, California	Tetra Tech (1976)
cold water	0.05	-	-	0.05	-	Lake Washington	Chen and Orlob (1975)
Diatom Blue	0.0015*	0.35-0.50**	-	0.4	-	Saginaw Bay, Lake Huron	Bierman (1976)
Blue Green	0.0015*	0.35-0.50**	-	0.15	-	Saginaw Bay, Lake Huron	Bierman (1976)

* = 0.0015 $(day\text{-}°C\text{-}mg/l)^{-1}$

** = 0.35-0.50 mg algae/mg zooplankton -day

TABLE IV-7. VALUES FOR ENDOGENOUS RESPIRATION RATES OF PHYTOPLANKTON (DI TORO ET AL. 1971)

Organism	Temperature, °C	Endogenous Respiration Rate, Day^{-1} ($Base_e$)
Nitzschia closterium	6	0.035
	35	0.170
Nitzschia closterium	20	0.08
Coscinodiscus excentricus	16	0.075
	16	0.11
Natural association	2	0.03
	18	0.12
	2.0	0.024±0.012
	17.9	0.110±0.007

TABLE IV-8. VALUES FOR GRAZING RATES OF ZOOPLANKTON (DI TORO ET AL. 1971)

Organism	Reported Grazing Rate	Grazing Rate, Liter/Mg Dry Wt.-Day
Rotifer		
Brachionus calyciflorus	0.05-0.12[a]	0.6-1.5
Copepod		
Calanus sp.	67-208[b]	0.67-2.0
Calanus finmarchicus	27[a]	0.05
Rhincalanus nasutus	98-670[a]	0.3-2.2
Centropages hamatus		0.67-1.6
Cladocera		
Daphnia sp.		1.06
Daphnia sp.		0.2-1.6
Daphnia magna	81[a]	0.74
Daphnia pulex	57-82[a]	0.2-0.3
Natural association		
Georges Bank	80-110[b]	0.8-1.10

[a] ml/animal-day

[b] ml/mg wet wt-day

RECOMMENDED FORMULATIONS

Selection of appropriate formulations for reservoir phytoplankton dynamics is a difficult and complex task. There is not necessarily a "correct" or "best" set of formulations. The processes which occur, and the state variables which are important, depend to some extent on site-specific conditions and on the particular purpose of the modeling exercise.

Site-specific conditions such as depth; circulation patterns; nutrient concentrations; and types of algal, zooplankton and fish species present can all affect the processes which occur and their relative importance. Thus, the need to model various processes may vary. For example, a reservoir which does not stratify does not need a three-dimensional transport model. A reservoir that strongly stratifies and results in an anaerobic hypolimnion may need a whole new set of formulations to describe the anaerobic processes which occur. Reservoirs with an excess of nutrients may be modeled without considering the effect of nutrient concentrations on growth rates, and thus eliminate a great deal of model complexity. Similarly, highly turbid reservoirs may limit algal production because of light transmission. The presence of zooplanktiverous fish may have a marked affect on phytoplankton production by reducing the phytoplankton predators.

One of the most important steps in constructing any model is the selection of processes which are important in the prototype. Models can aid in this selection by formulating processes and testing the sensitivity of model results to a range of assumptions.

The following discussion summarizes important considerations in selecting formulations for use when the pertinent process is deemed to be important in the prototype.

Transport

Transport includes advective flows, dispersion, and organism behavior. A number of hydrodynamic circulation models are available, and should be selected based on the size and circulation patterns of the prototype. Organism behavior, however, has not been well defined mathematically. Algal settling rates (or buoyancy) have not been studied in sufficient detail to write reliable formulations. Most models generally use a constant rate, although there has been some attempt to relate sinking rates to either available light or growth rate. Similarly, fish movements are difficult to prescribe mathematically. Presently, the best approach appears to be to assign preference factors based on food availability and temperature.

Algal Production

Rates of algal production depend on temperature, light, and nutrient availability. Although temperature effects are complex and it is not clear that modifying the maximum specific growth rate as a function of temperature is necessarily valid when used under conditions of light or nutrient limitations, the best approach seems to be an arbitrarily defined function for each species which has an increasing segment, an optimum and a decreasing segment. Such functions must be based on data and can consist of a simple "look up" table.

The effect of light on algal growth rates has been described with a number of different formulations as discussed earlier. All of the formulations discussed give an adequate description of observed behavior. Selection of a particular expression depends largely on personal preference and mathematical tractability. One of the simplest, which was used by Tetra Tech (1979), averages total daily surface radiation and integrates over depth to obtain:

$$Llim = \left(1.5\right)\left(light\right)\left(\frac{\Delta z - \frac{1}{\gamma}\left[\ln\left(1 + \frac{KI_i}{I_o} e^{\gamma z_2}\right) - \ln\left(1 + \frac{KI_i}{I_o} e^{\gamma z_1}\right)\right]}{\Delta z}\right)$$

where Llim = light limiting factor

light = daylight hours/24

I_o = average daily incident light intensity divided by 3/4 (light) ($Cal/m^2 \cdot s$)

Δz = thickness of element (m)

γ = total light attenuation coefficient (m^{-1})

KI = Michaelis-Menten half-saturation constant for light ($Cal/m^2 \cdot s$)

This value for the light limiting factor is then used in the growth rate expression.

Nutrient-growth rate relationships have been the most extensively studied and offer the widest choice of approaches. For simpler applications, the conventional Monod expression is considered adequate. However, for situations where uptake and growth are clearly distinct in time the formulations discussed by Bierman are more appropriate. The simpler expressions offer the advantage of more data being available for estimation of half-saturation constants.

It is recommended that the minimum of the various rate limiting factors (light, nitrogen, phosphorus, silicon) be used to reduce the maximum specific growth rate at each computational time step.

Algal Loss

Loss of algal cell biomass results from respiration, sinking, and grazing as well as heterotrophic degradation by bacteria. Most model formulations consider the loss rates as they occur in active viable cells. Little attention has been given to modeling viral attack or decomposition following a bloom.

Endogenous respiration is typically modeled as a first order process with a temperature dependent rate coefficient. Differentiation of

respiration into active and standard adds a complexity which is presently not supported by available data. It should be noted that the Workshop conclusions pointed out the need for more research emphasis on loss processes as opposed to production processes.

Formulations describing losses due to grazing can range from simple to very complex, depending on model formulation for zooplankton and fish production. The simplest, and probably most appropriate at this point in time, is to simply apply the zooplankton (or fish) grazing rate as a direct loss to the particular phytoplankton groups being grazed.

V. RESEARCH NEEDS

It has become apparent that our ability to write equations and provide computer programs to solve them has surpassed our knowledge of biochemical processes which occur in aquatic ecosystems. However, a general research approach which is interactive with model applications, field studies and laboratory studies could be very beneficial in providing the knowledge and tools necessary for effective reservoir planning and management.

The use of model sensitivity analysis can be valuable in determining which processes and/or coefficients are most important and formulating specific questions for the limnologist. As is true for most ecosystem models, reservoir models are used for four major purposes:

- To formalize our concepts about how reservoir ecosystems function.
- To identify testable hypotheses about how reservoir ecosystems function.
- To provide a means for evaluating and managing reservoir operation for a broad range of uses and for a wide variety of variables that otherwise would not be easy to understand in their entirety.
- To formulate sampling programs in space and time and to list the appropriate data needs.

These purposes exemplify research needs based on theory and application. Also, the application of knowledge gained from such research is implied. Each author in the workshop listed or suggested research needs based on their experience, and these are discussed briefly in the following paragraphs.

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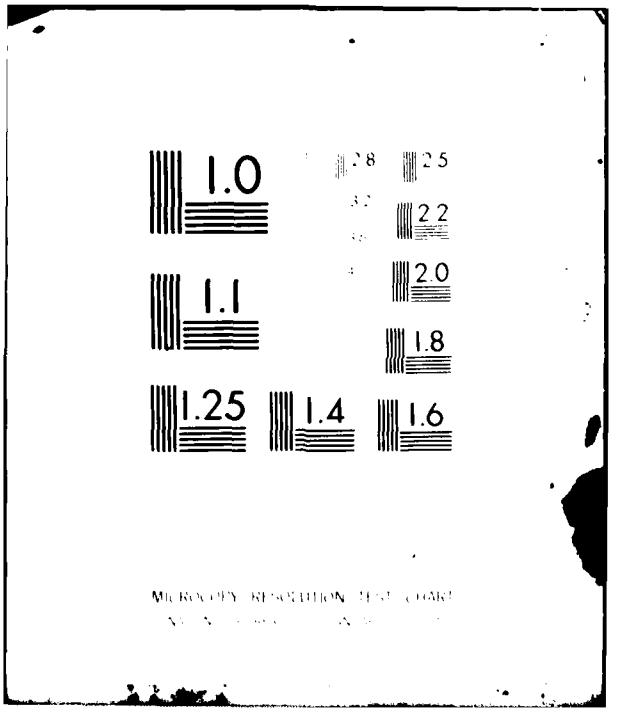
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PHYTOPLANKTON REMOVAL PROCESSES

Most research efforts have emphasized photosynthesis and algal production rates. The various factors affecting loss rates have been studied in much less detail. Thus, recycling of nutrient material and phytoplankton loss rates are processes that require research. Bierman discusses recycling as follows:

> "More research is needed on the nature of the recycle processes for phosphorus and nitrogen that occur as a result of both predatory and nonpredatory phytoplankton death in the water column. A closely related need is for more research on the factors controlling nitrogen fixation and subsequent recycle of available nitrogen. These recycle processes can supply a substantial portion of the nutrient requirements for summer blooms of nuisance blue-green algae in enriched reservoirs and impoundments. Without adequate knowledge of recycle processes, it is difficult to relate the occurrence of such blooms to external nutrient loadings and ambient nutrient concentrations."

Lehman felt that phytoplankton loss rates caused by zooplankton have been modeled very inaccurately. Consequently, model results diverge from actual measurements. Lehman states:

> "We are at a stage where our ability to model the effects of zooplankton on phytoplankton communities will profit from easily identified experiments and continued simulation efforts, too. First, mechanisms and adaptations for feeding need to be evaluated in light of the discovery by Mayzaud and Poulet (1978) that the filter feeders change their digestive physiology in response to their food supply. Efforts are needed to quantify the actual determinants of feeding rates, and to examine how the animals respond to changes in the quality of their food supply. This avenue will prove far more useful than research directed toward finding values for the fictitious parameters of most current models. Rates of assimilation should be measured for mixtures of foods as well as for single food types to provide the guides for more realistic models. If ingestion really is controlled by volumetric constraints, then experiments will show it, and model formulations will be improved. Most importantly, rates of nutrient remineralization due to the activities of the

zooplankton must be quantified for animals fed on diets of different quality and abundance. Experimental design is critical, because uptake and release of nutrients proceed simultaneously and inseparably, but this is one area where models and empiricism work together very well (Lehman, in press)."

Di Toro discussed another aspect affecting phytoplankton distribution patterns. He presented data showing that the effects of vertical and horizontal transport were substantial. Relationships between vertical dispersion algal settling velocity and depth of the euphotic zone were defined. Also, wash out due to advective flows can be important. His conclusions implied that these processes must be studied using actual data to determine the need for modeling these processes.

Similarly, Harris provided data on Hamilton Harbour in Lake Ontario that argues for the need for integrated models of mixing phenomena and the vertical distribution of phytoplankton. He illustrated processes that showed the interaction of light, temperature and nutrient supply in controlling phytoplankton community population density.

The application of these results is often somewhat difficult to perceive. However, Poppe et al. showed that some managerial options for control of phytoplankton blooms could be based on considerations of loss rates and nutrient recycling and on dispersion properties of reservoirs. Methods for applying these processes require additional development. Some of these processes are reservoir release methods (timing of release and vertical location of release) and biological control methods (zooplankton grazing). Also, accurate manager level models for controlling phytoplankton blooms using existing technology need development; Poppe et al. state that these models would have immediate application to problems that result from phytoplankton blooms.

PHYTOPLANKTON PRODUCTION PROCESSES

Light, temperature and nutrient supply have all been identified as important state variables that control phytoplankton production processes. As defined by both Megard and Harris, the maximum phytoplankton production is a function of these variables. Despite intensive research activity over the last few decades on the effects of these variables on phytoplankton growth, many questions remain to be answered. The analysis of the U.S. EPA National Eutrophication Survey data indicates the need for research on how light, temperature and nutrients control phytoplankton succession and how chlorophyll varies as a measure of phytoplankton production and biomass. Because models apply these processes and state variables without clear understanding of how they control algal growth some significant research on these processes remains to be accomplished.

For example, Bierman identified silicon kinetics and nitrogen fixation as important areas for needed research. Generally, he felt that nutrient uptake and feedback control mechanisms should be elucidated more clearly. Also, Lawley stated that nitrogen fixation was an important process in water quality degradation of Texas reservoirs.

Goldman concluded that considerable research on temperature effects on phytoplankton nutrient assimilation processes was needed. Because of temperature-caused density stratification of reservoir waters, the role of temperature both on a seasonal and vertical basis needs to be well understood in order to evaluate phytoplankton growth in reservoirs.

Both Megard and Harris discussed the process of photoinhibition of phytoplankton by high light intensities; because models apply this process without clear understanding of mechanisms, research on methods of measurement and evaluation of impact is required.

Use of laboratory culture methods such as bioassays to explain nutrient relationships in general and to develop relationships for specific reservoir sites can be invaluable. However, Porcella and Cleave

recommended that continuous culture techniques be developed further for assessing reservoir conditions and the role of nutrients and toxicants in controlling phytoplankton. It is felt that continuous culture techniques more accurately duplicate the natural condition of reservoirs than do the common, more easily performed batch bioassay. Also, they recommended that algal bioassay batch studies be evaluated so that potential growth can be estimated relative to actual growth in the prototype. Research on this relationship is required.

As discussed by Kimmel and White, in situ estimation of phytoplankton condition, such as DCMU enhanced fluorescence response, appears worthy of further evaluation in field studies. Specific research topics include study of the effects of diel flux in fluorescence and photosynthetic capacity, species composition, and the effects of high light intensity. This may be a promising approach for assessing photoinhibition effects in reservoirs and other natural surface waters.

APPLICATIONS TO PROTOTYPE RESERVOIRS

Bierman suggested that:

> "In the general sense, the most urgent research need in the subject area is more experience in the application of phytoplankton simulation models to extensive sets of field data for different types of physical systems. This is the only means of establishing definitive criteria for choosing an appropriate set of phytoplankton-nutrient kinetic mechanisms for a given application."

Related to this concept is the statement by Scavia about model validation. Not only should model output be compared to actual data but model processes need to be validated. Reported Scavia:

> "After initial calibration of the model described above to state variables measured during IFYGL, I generated the phosphorus cycling diagram shown in Figure 9a and began to examine the cycling rates. I found that, although the model

adequately represented the state variables in Lake Ontario, its estimates of several process rates were very much lower than experimentally and theoretically derived rates. By recalibrating the model while still keeping coefficient values within the broad "acceptable ranges," I was able to obtain more realistic process rates and at the same time maintain a good calibration to state variables (Figure 9b).

Conclusions concerning the relative importance of particular processes in the cycling of phosphorus, based on model output that was not validated on the process level (e.g., Figure 9a), would be quite different from conclusions based on the more realistic simulation (e.g., Figure 9b)."

The whole process of model concept development, validation, and application requires refinement. Megard stated that processes related to light, temperature, nutrients, grazing, predation, respiration, excretion, and sinking require research. This is undoubtedly true, but the application of models to practical control problems may not require such sophistication and development. Sensitivity analysis and application of models to actual data sets of sufficient quantity would serve to identify those variables that are important. Application of rarefaction techniques to data and also to processes might simplify the managers problem in dealing with such a broad range of variables that are difficult to comprehend in toto. As Bierman concluded:

"It should be recognized that the practical constraints of budget and time frame will frequently preclude the application of the most sophisticated kinetic models. Accordingly, emphasis should be placed on the further development of kinetic mechanisms which avoid unrealistic data requirements and computational complexity, yet still constitute reasonable approximations of the major dynamic features of the system. Objectives need to be well-defined at the outset of a particular application and the inherent assumptions and limitations of the kinetics model used must be respected. Even the simplest kinetic models can be of great value in providing a conceptual framework for experimental design and data interpretation."

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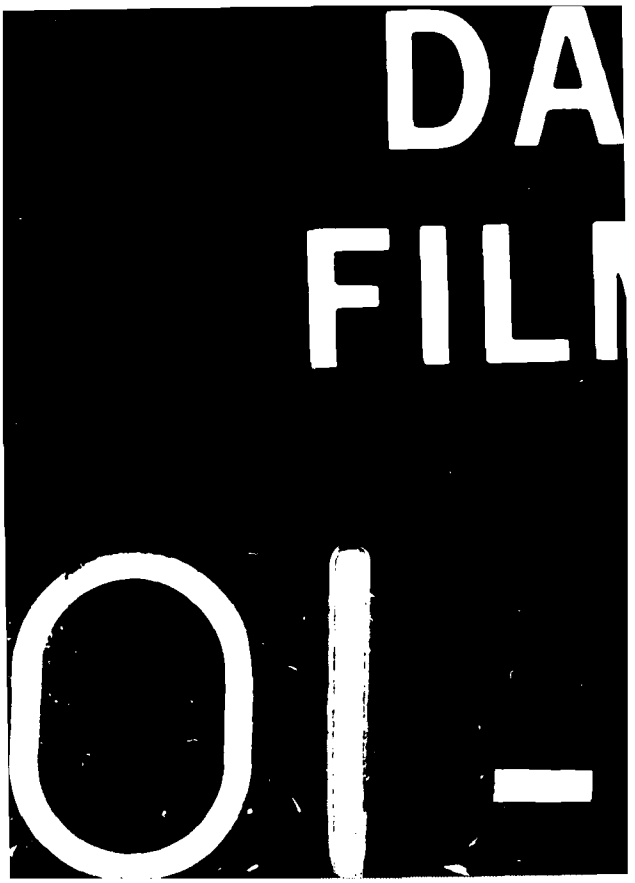
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